

EXPERIMENTS IN HEARING

McGRAW-HILL SERIES IN PSYCHOLOGY

CLIFFORD T. MORGAN, *Consulting Editor*

BARKER, KOUNIN, AND WRIGHT · Child Behavior and Development
VON BÉKÉSY · Experiments in Hearing
BLUM · Psychoanalytic Theories of Personality
BROWN · The Psychodynamics of Abnormal Behavior
BROWN AND GHISELLI · Scientific Method in Psychology
CATTELL · Personality
CRAFTS, SCHNEIRLA, ROBINSON, AND GILBERT · Recent Experiments in Psychology
DEESE · The Psychology of Learning
DOLLARD AND MILLER · Personality and Psychotherapy
DORCUS AND JONES · Handbook of Employee Selection
FERGUSON · Personality Measurement
FERGUSON · Statistical Analysis in Psychology and Education
GHISELLI AND BROWN · Personnel and Industrial Psychology
GRAY · Psychology Applied to Human Affairs
GRAY · Psychology in Industry
GUILFORD · Fundamental Statistics in Psychology and Education
GUILFORD · Psychometric Methods
GUILFORD · Personality
HAIRE · Psychology in Management
HIRSH · The Measurement of Hearing
HURLOCK · Adolescent Development
HURLOCK · Child Development
HURLOCK · Developmental Psychology
JOHNSON · Essentials of Psychology
KARN AND GILMER · Readings in Industrial and Business Psychology
KRECH AND CRUTCHFIELD · Theory and Problems of Social Psychology
LEWIN · A Dynamic Theory of Personality
LEWIN · Principles of Topological Psychology
MAIER AND SCHNEIRLA · Principles of Animal Psychology
MILLER · Language and Communication
MISIAK AND STAUDT · Catholics in Psychology: A Historical Survey
MOORE · Psychology for Business and Industry
MORGAN AND STELLAR · Physiological Psychology
PAGE · Abnormal Psychology
REYMERT · Feelings and Emotions
SEASHORE · Psychology of Music
SHAFFER AND LAZARUS · Fundamental Concepts in Clinical Psychology
SIEGEL · Nonparametric Statistics: For the Behavioral Sciences
STAGNER · Psychology of Personality
TOWNSEND · Introduction to Experimental Method
VINACKE · The Psychology of Thinking
WALLEN · Clinical Psychology: The Study of Persons
ZUBEK AND SOLBERG · Human Development

John F. Dashiell was Consulting Editor of this series from its inception in 1931 until January 1, 1950.

EXPERIMENTS IN HEARING

Georg von Békésy

TRANSLATED AND EDITED BY

E. G. Wever



McGRAW-HILL BOOK COMPANY, INC.

New York Toronto London

1960

152.2
BEIC

EXPERIMENTS IN HEARING

Copyright © 1960 by the McGraw-Hill Book Company, Inc. Printed in the United States of America. All rights reserved. This book, or parts thereof, may not be reproduced in any form without permission of the publishers. *Library of Congress Catalog Card Number 59-9411*

4324

THE MAPLE PRESS COMPANY, YORK, PA.

Bureau Ednl.	Research
DAVID H.	ING COLLEGE
Dated...	~~14~~ 25.4.60
Accs. No.....	1475

S.O.B.R.T. West Berlin

Date

Acc No. 1475

PREFACE

This book brings together in one volume the chief results of a series of experimental studies on hearing and related problems extending over a period of 34 years. The earlier experiments, from 1924 to 1946, were carried out in the Royal Hungarian Institute for Research in Telegraphy in Budapest, those in 1947 in the Department of Telegraphy and Telephony of the Royal Institute of Technology in Stockholm, and the ones since that time in the Psycho-acoustic Laboratory of Harvard University. I am deeply grateful to the directors and staffs of all these institutions, and especially to Professor S. S. Stevens and Professor E. B. Newman, for their generous provision of facilities and technical help. In my work at the Psycho-acoustic Laboratory I am especially indebted to Mr. Ralph Gerbrands and Mr. Rufus L. Grason for their assistance in the development of mechanical and electrical equipment, to Miss Geraldine Stone for aid in the preparation of the papers published in English, and to Mrs. Elizabeth Gardner for her work in the production of drawings. Research in hearing is of such a complex and exacting nature that it would be difficult to proceed without advantage of the knowledge and skills of many other persons.

The original articles appeared in numerous technical journals, access to many of which is now difficult. More than half of them were written in German, the others in English, and all necessarily adhered to the special requirements of the various journals and editors. For this book the German articles have been translated into English, and all have been edited to produce a uniform style.

For this work I am indebted to Professor E. G. Wever, and it is proper to say that this presentation was made possible by his willingness to assume the task. Probably many persons cannot appreciate the labor that is involved in an undertaking of this kind to the extent that I do, who have shifted about in this troubled world to so many countries and have learned and forgotten so many languages. It is almost a unique privilege to have this aid from someone working in the same field of research and conversant with its problems and technicalities.

It should be emphasized that the presentations adhere to the original articles, and the interpretations of problems and results reflect the evidence at hand when the research was carried out. In one or two instances, when later work has led to a change in viewpoint, this fact is pointed out in a footnote. Also a few typographical and other errors have been corrected.

The articles are grouped by subject, and the arrangement bears only a limited relation to the temporal order in which the experiments were

performed. Part 1 is introductory. It presents two short chapters of new material on the nature of auditory problems and the historical development of our knowledge about the anatomy of the ear, and then includes two other chapters on anatomical techniques and experimental methods. The technical material of these last two chapters has been extracted from the experimental articles and assembled here so as to avoid needless repetition later on. The remainder of the book consists of the articles in their original form except for the extractions just mentioned and a few other deletions that are referred to at the proper places. Part 2 is concerned with the process of sound conduction in the ear, Part 3 with several aspects of the psychology of hearing, and Part 4 with the mechanical and physiological processes of the cochlea and its associated nervous system.

I should like to express my deepest gratitude to S  zanne Wever for the typing of the manuscript. The care and precision with which she performed this task contributed greatly to reduce the number of errors.

Georg von B  k  sy

ACKNOWLEDGMENTS

Acknowledgment is made to the following publishers for permission to reproduce the articles included here.

The Journal of the Acoustical Society of America
American Institute of Physics
New York, New York

Akustische Zeitschrift and Physikalische Zeitschrift
S. Hirzel Verlag
Stuttgart, Germany

Annalen der Physik und Zeitschrift f  r technische Physik
Verlag von Johann Ambrosius Barth
Leipzig, Germany

Acta oto-laryngologica
Swedish Medical Society
Stockholm, Sweden

Elektrische Nachrichten Technik
Springer Verlag
Berlin, Germany

Forschungen und Fortschritte
Nachrichtenblatt der deutschen Wissenschaft und Technik
Berlin, Germany

Laryngoscope
The Laryngoscope Company
St. Louis, Missouri

The Proceedings of the National Academy of Sciences
University of Chicago Press
Chicago, Illinois

Review of Scientific Instruments
American Institute of Physics
New York, New York

Science
American Association for the Advancement of Science
Washington, D.C.

Transactions of the American Microscopical Society
American Microscopical Association
Columbus, Ohio

CONTENTS

Preface	v
-------------------	---

PART 1. INTRODUCTION

1. Problems of Auditory Research	3
2. The Anatomy of the Ear	11
3. Anatomical Techniques	19
4. Experimental Apparatus and Methods	33

PART 2. CONDUCTIVE PROCESSES

5. The Action of the Middle Ear	95
Movements of the Auditory Ossicles.	95
Physics of the Middle Ear	104
Differences in Sound Pressure between the Cochlear Windows	115
6. Bone Conduction	127
Nature of Bone Conduction	128
Absolute Bone-conduction Threshold	148
Vibration of the Head in a Sound Field	163
Structure of the Middle Ear and Hearing of the Voice by Bone Conduction	181

PART 3. THE PSYCHOLOGY OF HEARING

7. Auditory Thresholds	207
Just-noticeable Differences of Amplitude and Frequency	207
Fechner's Law and Its Significance	238
Low-frequency Thresholds for Hearing and Feeling	257
Effects of the Head and External Auditory Meatus on the Sound Field	267
8. The Spatial Attributes of Sounds.	272
The Sensation of Direction	272
Perception of the Distance of a Sound Source	301
9. Problems of Distortion.	314
Clicks and the Theory of Hearing	314
Audibility of Transients	321
Nonlinear Distortion in the Ear	332
Acoustic Roughness	344
Fatigue Phenomena	364

10. Room Acoustics.	369
Optimum Reverberation Time	369
Audibility in Small Concert Halls	383
Effects of an Absorbent Surface on a Sound Field	392

PART 4. COCHLEAR MECHANICS

11. The Pattern of Vibrations in the Cochlea	403
Vibratory Pattern of the Basilar Membrane	404
Vibrations of the Cochlear Partition in Preparations and Models	429
Resonance and Decay Processes in the Cochlear Partition	446
Variations of Phase along the Basilar Membrane	460
Elasticity of the Cochlear Partition	469
Direct Observation of the Vibrations of the Cochlear Partition	480
12. Wave Motion in the Cochlea	485
Mechanical Properties of the Organ of Corti	485
Frequency Analysis in the Cochleas of Various Animals	500
Paradoxical Wave Travel along the Cochlear Partition	510
Simplified Model to Demonstrate Energy Flow and Traveling Waves	524
13. Frequency Analysis and the Law of Contrast	535
Frequency Analysis in the Human Cochlea	535
Current Status of the Theories of Hearing	539
Human Skin Perception of Traveling Waves	547
Sensations on the Skin Similar to Auditory Phenomena	568
Neural Volleys and Similarities between Tonal and Cutaneous Sensations	590
Funneling in the Nervous System and Its Role in Loudness and Sensory Intensity on the Skin	609
14. The Electrophysiology of the Cochlea	635
Direct Potentials and Energy Balance of the Cochlear Partition	636
Resting Potentials within the Cochlear Partition	647
Pattern of Electrical Resistance in the Cochlea	654
Microphonics Produced by Touching the Cochlear Partition with a Vibrating Electrode	672
Place of Origin of Cochlear Microphonics	684
Shearing Microphonics Produced by Vibrations in the Cochlea	703
Author's Bibliography	711
References	714
Index	729

PART 1

INTRODUCTION

CHAPTER 1

THE PROBLEMS OF AUDITORY RESEARCH

The experiments with which this book is concerned were begun when the field of acoustics was just approaching its modern period. The rapidly growing science of electronics was providing new and precise instruments for the production and measurement of sounds, and many new methods were being worked out for registering the effects of sounds on the ear. Some of these methods were physical, others were physiological or electrophysiological, and still others were psychological, involving the observations of human subjects. All three types were utilized in the experiments that are reproduced here, and often all of



FIG. 1-1. A Persian miniature painting of the fifteenth century.

them were applied to the solution of a single problem. Because results always flow from the procedure that is used, and because there has been almost a revolutionary development of techniques in acoustics during the decades covered by these studies, this chapter will be devoted to a discussion of auditory problems in relation to methodology.

A primary consideration is the problem to be investigated, how it is approached, and how it is envisaged in relation to what is already known. It is possible to distinguish two forms of approach to a problem. One, which may be called the theoretical approach, is to formulate the problem in relation to what is already known, to make predictions or extensions on the basis of accepted principles, and then to proceed to test these hypotheses experimentally. Another, which may be called the mosaic approach, takes each problem for itself with little reference to the field in which it lies, and seeks to discover relations and principles that hold within the circumscribed area.

A close analogy to these two approaches may be found in the field of art. In the period between the eleventh and seventeenth centuries the Arabs and Persians developed a high mastery of the arts of description and portrayal, and they used the mosaic style. An example is given in Fig. 1-1, which shows a Persian miniature painting of a betrothal. The various persons and objects are represented individually, spread out as though on a carpet, and with little perspective or relation to one another.

Later, during the Renaissance, a new form of representation was developed in which the attempt was made to give unity and perspective to the picture and to represent the atmosphere. An example of this form of art is shown in Fig. 1-2.

When in a field of science a great deal of progress has been made and most of the pertinent variables are known, a new problem may most readily be handled by trying to fit it into the existing framework. When, however, the framework is uncertain and the number of variables is large the mosaic approach is much the easier.

Many of the experiments to be described in this book employed the mosaic approach, but when considered in connection with other experiments carried out subsequently by the author and by many other workers in this field they take on a broader meaning and perhaps now may be woven into a more general structure.

Of great importance in any field of research is the selection of problems to be investigated and a determination of the particular variables to be given attention. No doubt the verdict of history will be that the able scientists were those who picked out the significant problems and pursued them in the proper ways, and yet these scientists themselves would probably agree that in this phase of their work fortune played a highly important role. When a field is in its early stage of development the selection of good problems is a more hazardous matter than later on, when some general principles have begun to be developed. Still later, when the broad framework of the science has been well established, a problem will often consist of a series of minor issues.



FIG. 1-2. A woodcut of the Renaissance period, sixteenth century.

Problems arise in a variety of ways, and it is often worthwhile to list the forms that they may take. Thus we can distinguish the following:

1. The classical problem, which has had much effort expended upon it, but without any acceptable solution.
2. The premature problem, which often is poorly formulated, or is not susceptible to attack.
3. The strategic problem, which seeks data on which a choice may be made between two or more basic assumptions or principles.
4. The stimulating problem, which may lead to a reexamination of accepted principles and may open up new areas for exploration.
5. The statistical question, which may be only a survey of possibilities.
6. The unimportant problem, which is easy to formulate and easy to solve.

7. The embarrassing question, commonly arising at meetings in the discussion of a paper, and rarely serving any useful purpose.

8. The pseudo problem, usually the consequence of different definitions or methods of approach. Another form of pseudo problem is a statement made in the form of a question. It also is often the result of discussions in meetings.

It is frequently helpful to attempt to place a given problem in this array of possibilities, for such a classification may provide a hint as to the problem's significance, the difficulties involved in its attack, and the sort of solution that may be expected.

A considerable amount of scientific work consists in the repetition of

experiments previously performed by others. This is a particularly onerous task, partly because the conditions of the original experiment are not described in full, and because the motivation is poor. The original work was done with care and enthusiasm, but its repetition can be dull and uninspiring. Almost inevitably the work is rushed through.

In psychological experiments an important matter is the type and number of subjects. These two are usually related, and the investigator can use a small number of highly trained subjects for extended periods or a large number of slightly trained subjects for brief times. Both procedures have their uses according to the problem at hand. When basic phenomena have to be explored and the important variables identified it is best to use subjects that are trained as thoroughly as possible. A trained subject will show only limited variability, largely because he is able to keep his attention on the phenomena under investigation and to ignore irrelevancies. On the other hand, it may be of interest to discover the range of capacities in a population, and then it is obvious that a great many subjects are needed.

In any event, it is necessary to train every subject to some extent and to instruct him in the phenomena that are to be reported. Sometimes there are unexpected difficulties in this regard, as an example will make clear. In the experiments on loudness discrimination one of the subjects was a gypsy violinist. In the early part of the experiment his difference limens were enormous, far out of the range of the other subjects. His pitch limens, however, had about the usual values. After much probing it finally developed that he was paying little attention to loudness changes, and the reason for this was that in gypsy music only the pitch is considered an important variable and the loudness is kept relatively uniform. After this situation was understood by the subject, and deliberate training in loudness perception was carried out, his loudness limens fell to normal values.

In the research described in the following chapters the emphasis is upon obtaining numerical values. When such values are lacking it is hardly possible to make a decision among competing hypotheses. An example will make this point clear. Perhaps the most significant measurement in relation to the operation of the cochlea is that of the volume elasticity of the basilar membrane. This value alone can determine whether the basilar membrane vibrates according to a standing-wave theory, a traveling-wave theory, a resonance theory, or a telephone theory. It is not always easy, however, to decide what numerical values are of real importance. Usually a great deal of preliminary work is necessary to discover what variables or constants are of essential value.

There is also the question of the time to be expended in the obtaining of numerical values. One way of increasing precision and also of saving time is to make the presentations as automatic as possible. Of course a certain balance has to be struck between the time saved by automation and the time and effort that have to be expended in setting up the special equipment. However, there is an added gain in many experiments,

especially those involving psychological judgments, because the automatic arrangement helps in generating a stabilized atmosphere. In the writer's experience it is good practice in psychological investigations to have a subject in a room alone with the apparatus, with the instruction to press a button when he is ready to make an observation. The system is designed to make the presentation, record the subject's judgment on a paper strip, and then stop until the button is pressed once more. Under these conditions there is no distraction from the presence of another person, and the subject is able to choose the moment when he can give the task his full attention.

A real difficulty with automatic equipment is that it increases the number of data. As a consequence there is a pressure to use statistical methods in evaluating the results. This procedure can greatly alter the problem, or even transform it to something out of all resemblance to the original one.

In scientific work there is always a difficulty in deciding when an experiment should be considered as completed. Most experiments are begun with a definite goal in mind, and there is a strong impulse to stop when this goal is reached. If the goal is not reached on the first attempt the procedure is altered and improved, and this activity continues until the expected results are obtained. It is obvious that this behavior operates so as to bias the investigation in a certain direction. Mistakes that lead away from the goal are corrected; those that lead to it are unnoticed. If the variance of the experiment is large this procedure almost surely leads to wrong conclusions. The writer has found it profitable to carry on a series of experiments for a month or so beyond the point where everything seemed complete and ready for publication. Almost invariably this somewhat aimless working with the equipment has brought out new aspects of the problem and rounded out the final conceptions. Sometimes it has led to new kinds of observations.

It is particularly difficult to determine when a negative experiment should be concluded. It is hardly ever possible to prove the negative of a proposition, and it has come to be a rule of thumb to bring a piece of work to a close after negative results have been obtained ten times in succession. Yet someone has pointed out that ten consecutive failures to circumnavigate the globe did not prove that the earth was flat. Perhaps the most interesting negative experiment in the field of physics was the one concerned with perpetual motion. Hundreds of failures did not seem to be convincing. Yet out of these failures came the development of the three laws of thermodynamics. On the basis of these laws it became possible to make positive statements that could be either proved or disproved with a single experiment, and the result was a transformation of a long period of stagnation into one of great progress. The same has happened in other fields of science, and thus it is comforting that even failure may sometimes have its benefits.

One of the most important features of scientific research is the detection and rectification of errors. The writer believes that positive results and

failures ought to be discussed together. Only by such complete reporting can we get a true conception of a piece of work, of the manner of its development, and of the limitations of its principles.

One way of discovering errors is to repeat the same measurements by different methods. If the same results are obtained by widely differing methods we can feel reasonably confident of their reliability. A way of avoiding errors is to work in a team. The several members can supplement one another's skills and check the procedures. In team research, however, it often happens that the dull, routine work is left to the younger

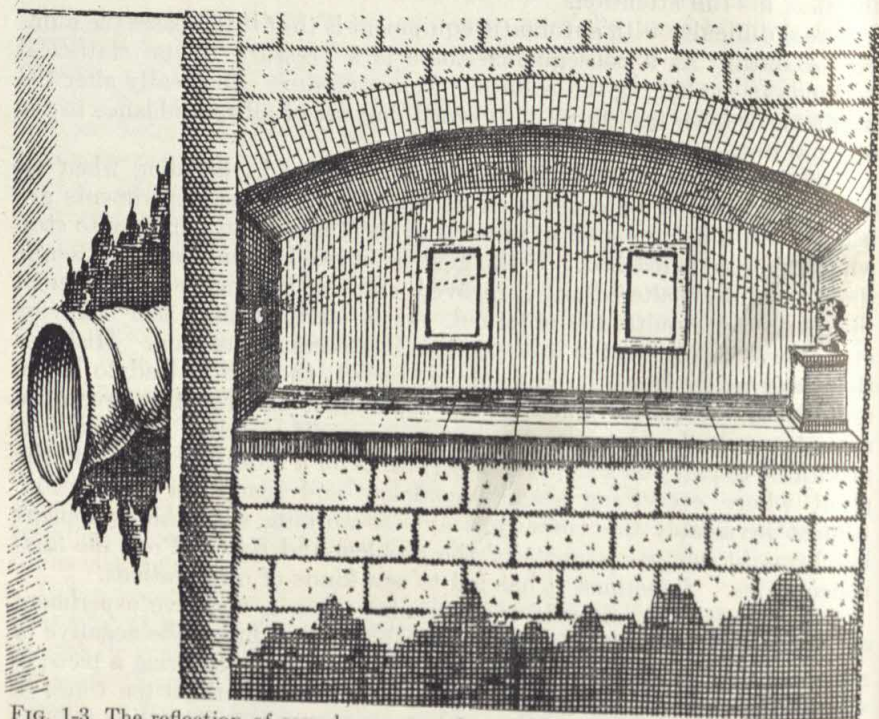


FIG. 1-3. The reflection of sound waves on the ceiling of a room, as represented by Kircher, 1650.

members and not checked by the more experienced. If, for example, the least able individuals are given all the calibrations to do, their mistakes can affect all the results.

Another way of dealing with errors is to have friends who are willing to spend the time necessary to carry out a critical examination of the experimental design beforehand and the results after the experiments have been completed. An even better way is to have an enemy. An enemy is willing to devote a vast amount of time and brain power to ferreting out errors both large and small, and this without any compensation. The trouble is that really capable enemies are scarce; most of them are only ordinary. Another trouble with enemies is that they sometimes develop

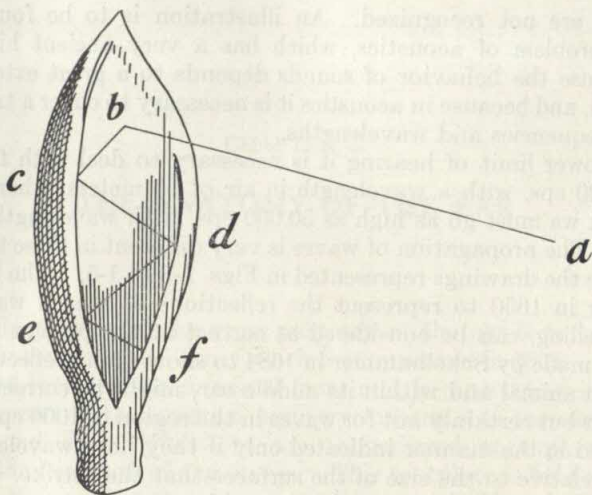


FIG. 1-4. The reflection of sound waves in the pinna of an animal, according to Schellhammer, 1684.

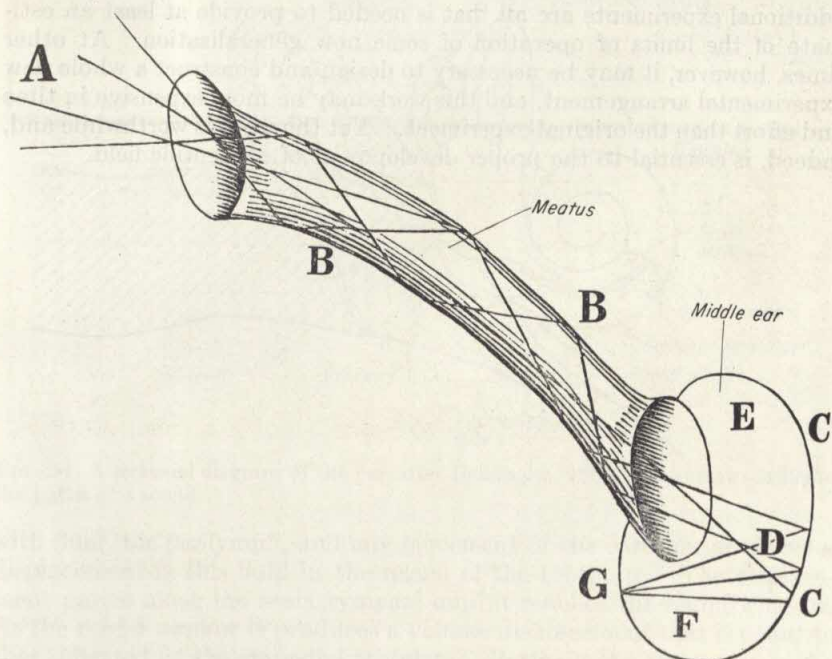


FIG. 1-5. The reflection of sound waves through the meatus and middle ear and their concentration on the cochlear window, according to Schellhammer.

into friends and lose a good deal of their zeal. It was in this way that the writer lost his three best enemies.

A further question concerns the boundaries within which a principle may be considered as valid. Serious errors can be made when such

boundaries are not recognized. An illustration is to be found in the following problem of acoustics, which has a very ancient history. It arises because the behavior of sounds depends to a great extent on the wavelength, and because in acoustics it is necessary to cover a tremendous range of frequencies and wavelengths.

At the lower limit of hearing it is necessary to deal with frequencies as low as 20 cps, with a wavelength in air of 15 meters, whereas at the upper limit we must go as high as 50,000 cps, with wavelengths as short as 6 mm. The propagation of waves is very different in these two ranges.

Compare the drawings represented in Figs. 1-3 to 1-5. The first, made by Kircher in 1650 to represent the reflections of speech waves on an elliptical ceiling, can be considered as correct at the present day. The other two, made by Schelhammer in 1684 to show sound reflections in the pinna of an animal and within its middle ear, might be correct for ultrasonic waves but certainly not for waves in the region of 1000 cps. Waves are reflected in the manner indicated only if they have wavelengths that are small relative to the size of the surfaces that they strike.

Many misunderstandings would be avoided if for every statement an indication was made of its expected range of application. At times a few additional experiments are all that is needed to provide at least an estimate of the limits of operation of some new generalization. At other times, however, it may be necessary to design and construct a whole new experimental arrangement, and this work may be more expensive in time and effort than the original experiment. Yet the work is worthwhile and, indeed, is essential to the proper development of a scientific field.

CHAPTER 2

THE ANATOMY OF THE EAR

A good description of the gross anatomy of the ear is to be found in Helmholtz's *Sensations of Tone*, which first appeared in 1863. The figure that he used includes the principal parts and is reproduced in Fig. 2-1. The air pressure in the external auditory meatus sets the eardrum into vibration, and these vibrations are transmitted through the larger ossicles to the footplate of the stapes. This footplate is held in the oval window of the cochlea by an annular ligament. The cochlea is filled

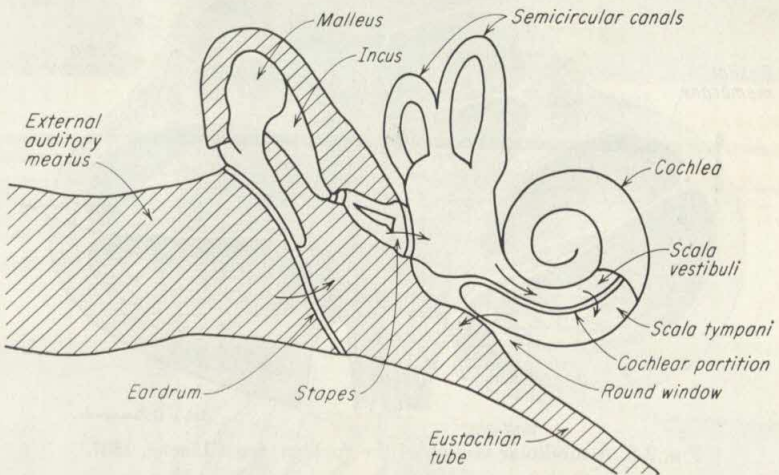


FIG. 2-1. A sectional diagram of the ear, after Helmholtz, 1863. The arrows indicate the paths of a sound.

with fluid, the perilymph, and any movement of the eardrum produces a displacement in this fluid in the region of the footplate. The displacement moves along the scala tympani until it reaches the round window. At the round window it produces a volume displacement that is equal to that initiated by the stapedial footplate. Between the two scalae is the cochlear partition, and the streaming of the fluid along this partition sets up a pressure difference across it. This pressure difference produces a deformation of the soft tissues comprising the partition, and among these are the sensory cells from which the stimulation is conveyed to the nerve endings.

Many of the general features of the ear's structure were discovered by

the pioneer anatomists of the sixteenth and seventeenth centuries. Not until the eighteenth century was well advanced, however, did the finer details begin to come to light. Some of the main steps in this development will be indicated by means of a series of pictures.

In Fig. 2-2 is a drawing published by Lincke in 1837. It is a cross section of the cochlea and represents the coiled form of the scala vestibuli and scala tympani. At the top of the cochlea is the helicotrema, an interconnection between the two scalae that keeps the fluid at the same pressure on each side of the basilar membrane. The entrance of blood vessels and the cochlear nerve through the modiolus is represented. On the upper left side of the cochlea is an indication that the partition

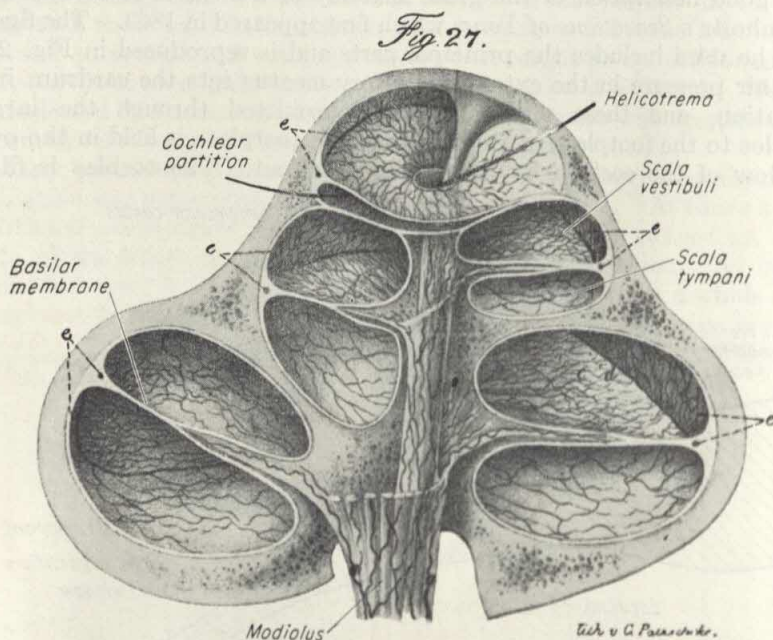


FIG. 2-2. A modiolar section of the cochlea, from Lincke, 1837.

between the two scalae consists of two membranes. It was in this enclosed space that Corti in 1851 discovered the organ named after him. At this time, however, the cochlear partition was usually represented as in Fig. 2-3. This sort of picture results from the opening of the cochlea and the escape of fluid, after which the tissues dry out.

A few years later the microscope was much improved and methods had been devised for the fixation of tissues. Corti then was able to see the single cells included in the cochlear partition in a manner indicated in Fig. 2-4. This was the first representation of cells lying on the basilar membrane. Compared with the structure as we know it today, this organ was greatly flattened. The flattening occurred because in the course of the preparation of the tissues the perilymph was allowed to escape, and the organ dried out and shrunk to a flat plate.

As the technique of fixation was improved further it became clear that these cells are not spherical but cylindrical. This feature may be seen in Fig. 2-5, which represents a drawing used at Harvard University around 1865. These cells are ciliated at one end, and are called hair cells. This figure also shows two pillars forming a tunnel between.

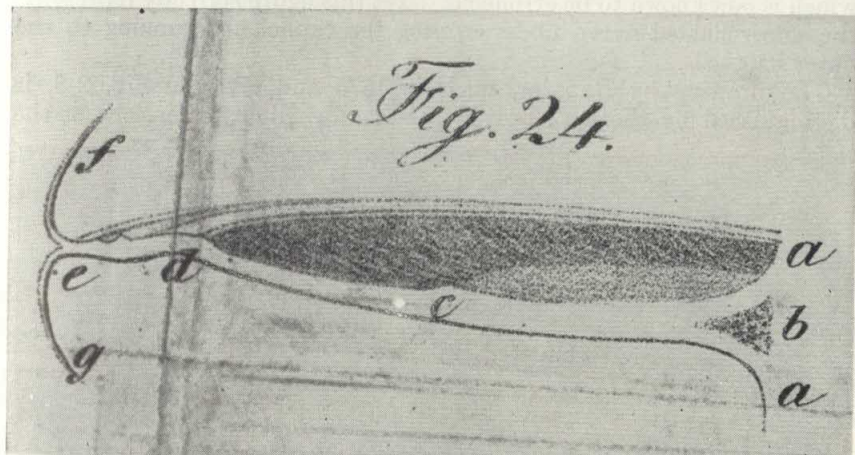


FIG. 2-3. The cochlear partition, from Lincke, 1837.

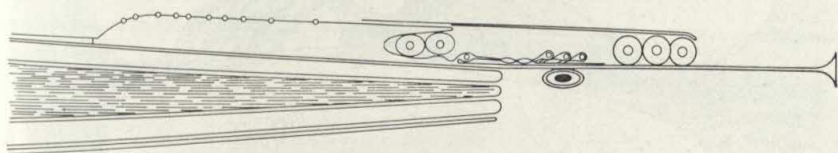


FIG. 2-4. Corti's drawing of the sensory apparatus, 1851.

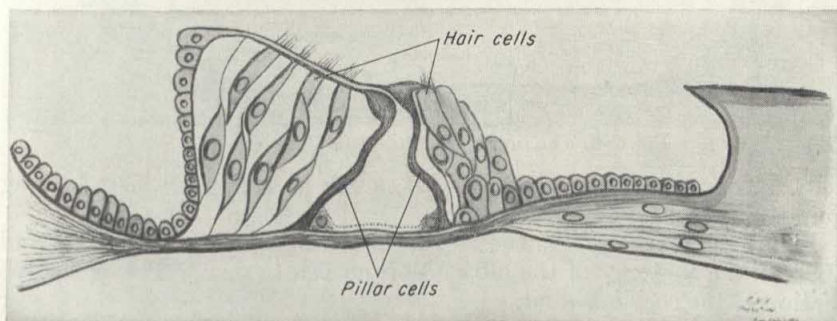


FIG. 2-5. The organ of Corti, from a drawing used at Harvard University around 1865.

The drawings made by Politzer in 1873 look almost like those of the present day. In the one shown in Fig. 2-6 the basilar membrane and Reissner's membrane are clearly represented. They divide the cochlear cavity into three tubes. That between Reissner's membrane and the basilar membrane is filled with a separate fluid, the endolymph. The

hair cells are covered over with the tectorial membrane, which as an artifact has been pulled away from the hair cells somewhat, leaving their cilia free. Politzer was uncertain about the proper form and position of the tectorial membrane, and in another picture, reproduced in Fig. 2-7, he portrayed it as extending to the external wall of the cochlea, which is now known to be erroneous. Yet this figure correctly represents the unmyelinated nerve fibers crossing the tunnel and running to the outer hair cells.

The drawing by Ranvier, made in 1875 and given in Fig. 2-8, is distinguished by the fact that it shows only slight distensions of the

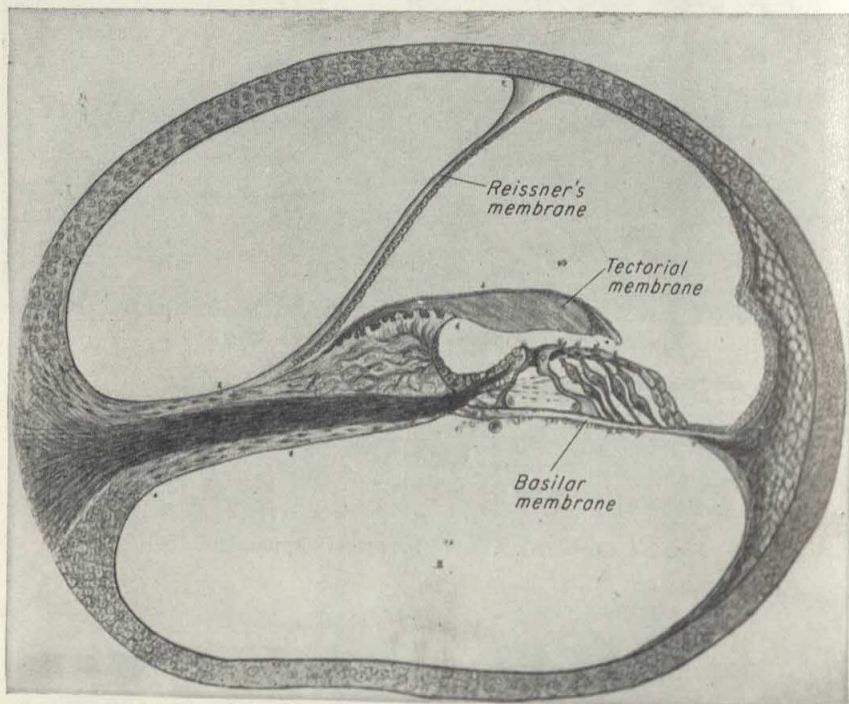


FIG. 2-6. The organ of Corti, after Politzer, 1873.

cells. The tectorial membrane is flat, much as it appears in the living guinea pig.

Figure 2-9 is taken from the monumental work of Retzius in 1881 and 1884 on the anatomy of the labyrinth from fish to man. This is a cross section of the cochlear duct.

By the end of the nineteenth century many theories had arisen regarding the process of hearing, and attention had become focused upon the hair cells and their enclosing structures. Renaut's drawing, presented as Fig. 2-10, shows how the hair cells hang in a perforated sheet, the reticular membrane. The tectorial membrane is supposed to rest on this sheet and to pull on the cilia during the movements of the basilar membrane. Kolmer (1) made beautiful drawings in color showing the

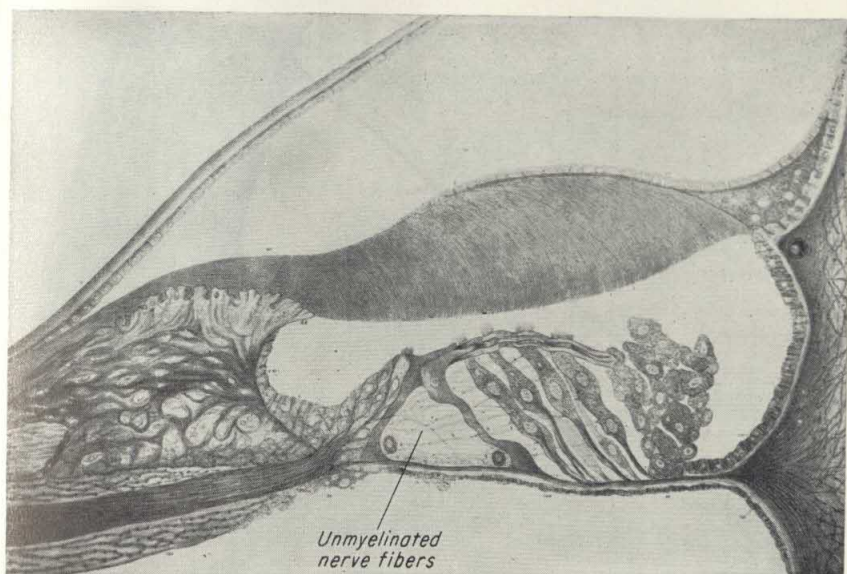


FIG. 2-7. A second representation of the organ of Corti, from Politzer, 1873.

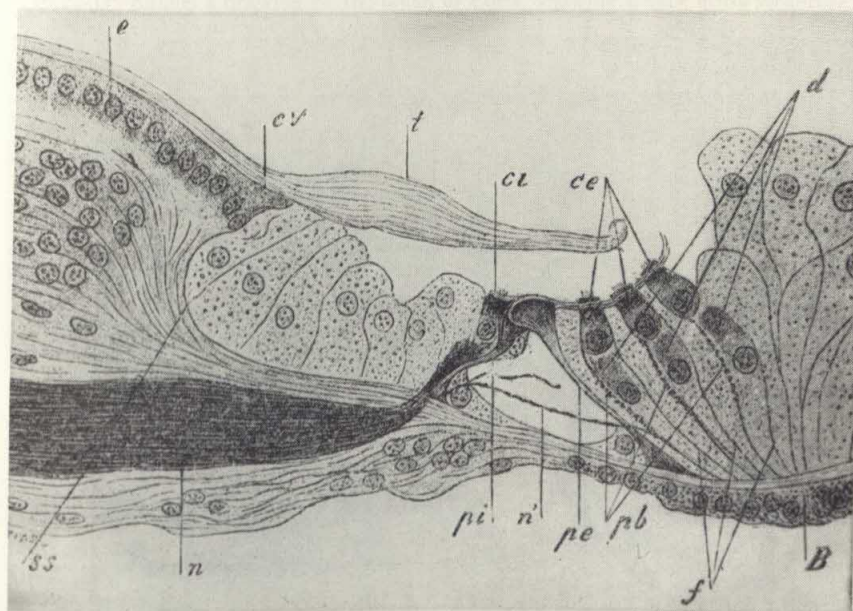


FIG. 2-8. Ranvier's drawing of the organ of Corti, 1875.

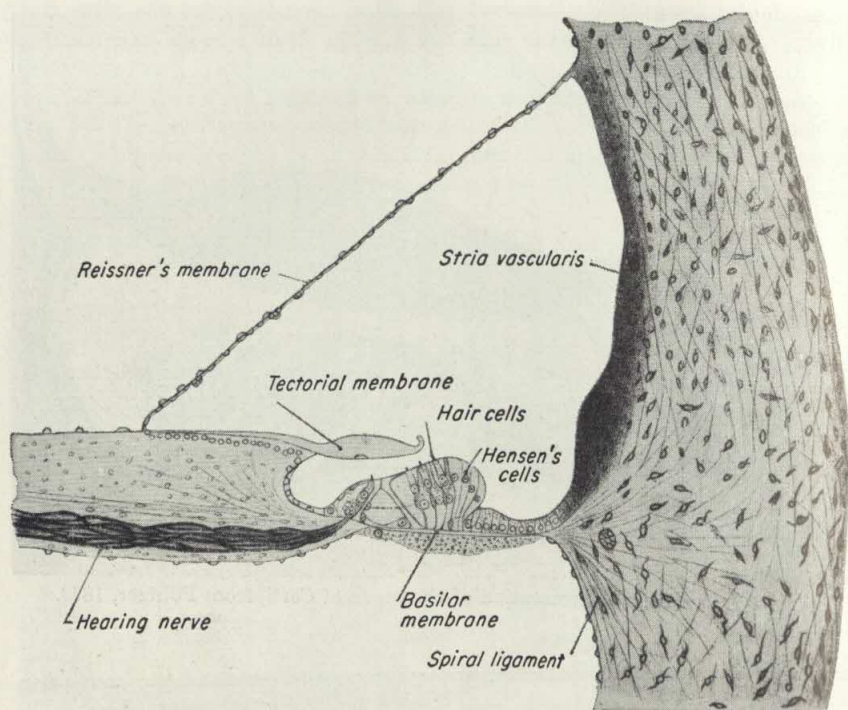


FIG. 2-9. The organ of Corti, after Retzius, 1884.

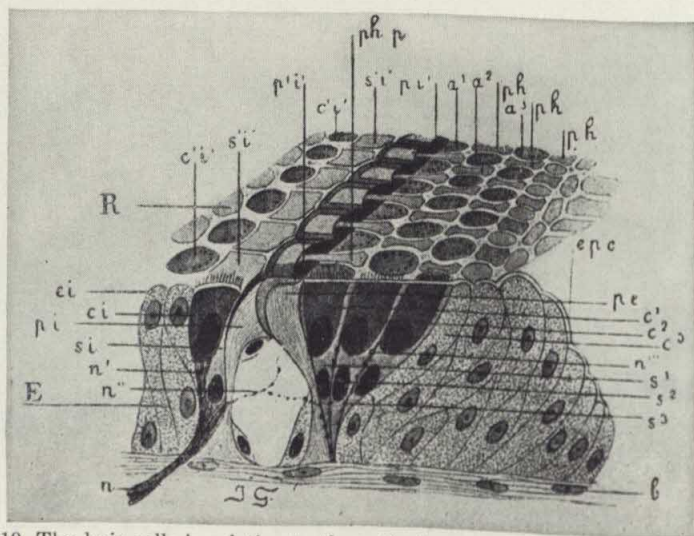


FIG. 2-10. The hair cells in relation to the reticular membrane, from Renault, 1899.

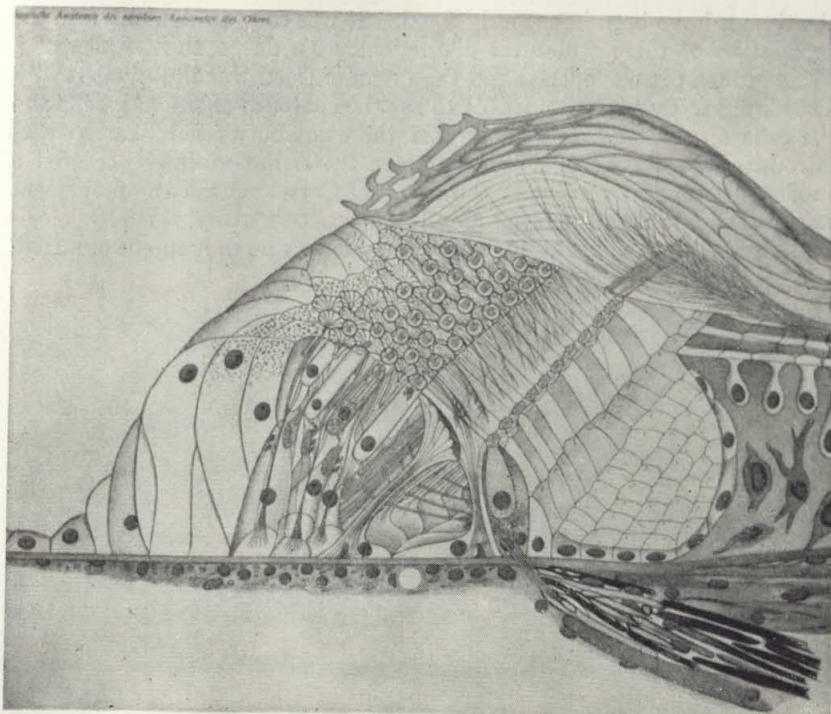


FIG. 2-11. Kolmer's drawing of the organ of Corti, showing details of its structure.

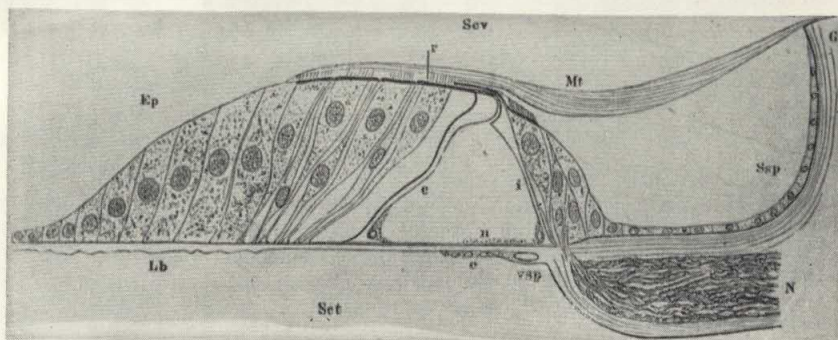


FIG. 2-12. Krause's drawing of the organ of Corti, 1927. The tectorial membrane as shown here approximates the normal form.

elaborate details of the structure, and one of them is given in Fig. 2-11. Here the tectorial membrane is swollen and lifted away from the hair cells. The swelling is an artifact produced in the process of fixation. The condition as shown in Fig. 2-12, in a drawing made by Krause in 1927, is more nearly normal.

The presence of artifacts, such as the swelling of the tectorial membrane found in many of the specimens that have been depicted here, means that

the tissues have been improperly fixed. It was easy to demonstrate the production of these structural distortions. To do so the cochlea of a living guinea pig was opened and the organ of Corti was illuminated with a slit lamp so that it was possible to see the contours of the hair cells and the cells of Hensen. If then any of the commonly used fixatives was introduced by means of a micropipette there immediately occurred a sudden jumping movement of the organ of Corti. Often the movement was so severe that the tectorial membrane was torn away. If physiological saline solution was introduced in the same way no movement occurred.

CHAPTER 3

ANATOMICAL TECHNIQUES*

The physical principles that have been developed and used with great success in engineering cannot be applied immediately to the mechanics of the ear. The tissues of the body are so much softer than the metals and other substances commonly employed in engineering that there can be no reduction of complex systems to a number of separate working parts, and no lumping of properties into elasticities, masses, and frictions as is done in engineering mechanics. This situation makes difficult a mechanical approach to the problems of hearing.

It is important that the physicist and engineer develop a sufficient understanding of these differences to appreciate the true problems and to discover the adaptation of the usual mechanical principles that must be made for the ear.

It is unfortunate that the study of anatomy has been much neglected in recent years. This is true even in medical schools, where the time devoted to this subject has steadily declined. Functional anatomy in particular has had little consideration, and though much attention has been given of late to electrophysiology there has not been any corresponding development of electroanatomy. Yet it is obvious that along with an understanding of the nature of electromechanical and electrochemical processes in tissues it is important to know what anatomical fields are involved.

Anatomy cannot be learned from books, for no description or set of static pictures can make clear the relations of the many complex parts and the great variety of individual variations. A dissection is a dynamic process, and this is as much true of dissection in a cadaver as that which occurs in surgery. Every step is a step of no return, and the dissector must proceed from one landmark to another. If he loses his orientation the result is usually unfortunate. Yet no anatomical book gives adequate attention to the landmarks, or shows which ones are the most useful. Everyone has to learn them for himself.

The learning of anatomy without tuition is a formidable task. The writer well remembers his experience of many years ago, when as a communications engineer he became interested in the anatomy of the ear and set out with hammer and chisel to study a human head. After several hours of hard work the piece of tissue became smaller and smaller,

* This chapter contains extracts from Arts. 38, 39, 42, 32, and 58, as listed in the Author's Bibliography at the end of the text.

and in the end faded away without affording even a glimpse of the inner ear structures. A histologist who had not been trained in the region of the ear recently reported that it took him a month to find the organ of Corti. This problem of orientation is much more difficult for the ear than for most bodily structures, because this organ is both complex and of small size, and is buried deeply in the temporal bone.

The following remarks are intended to stimulate physicists and telephone engineers to obtain some anatomical preparations of the ear and to study them, if they intend to deal with problems of hearing. The mechanics of the ear is so complicated that it can be described only with great difficulty. Almost always an examination of the actual conditions leads to entirely unexpected and novel points of view.

Though the techniques of dissection for medical purposes have been highly developed, there is no technique at all for dissecting small organs such as the middle ear and the cochlea. This is true in part because the available instruments are unsuitable for a direct investigation of these organs. The general practice is to study such structures only histologically, by means of serial sections. This situation has had a serious effect upon the development of the physiology of hearing and the pathology of the ear, for the observation of the fresh organ discloses many features that are lost in the course of histological preparation.

An attempt was made, therefore, to develop tools that would permit the sure and speedy preparation of specimens of small dimensions. This would give a kind of microanatomy as an intermediate stage between histology and standard methods of dissection.

Fresh temporal bones are to be obtained from the prosector of a large hospital. Nearly all the soft tissue must be removed from the bones, leaving only the inner half of the cartilaginous meatus. It is often desirable to use the temporal bones of newborn infants in the study of the cochlea, because these bones are not calcified and may be cut with a scalpel.

Because the instruments used by telephone engineers can neither be cleaned nor disinfected thoroughly, the danger of infection is greater in the physical laboratory than in an anatomy room. Especially to be avoided are tissues from persons that have died of typhus or sepsis. The preliminary work can be done with rubber gloves, which are put on after using talcum powder on the hands so as to avoid abrasions. For delicate dissections, however, it is necessary to work without gloves. To avoid infection, any minor scratches on the hands should be treated with tincture of iodine and given a protective covering of collodion. If there are major cuts all dissection should be avoided. However, many persons can become infected even though the skin is not broken, evidently through the pores, and it is well to rub the hands with petroleum jelly containing 2 per cent resorcinol provided that the person is not allergic to this substance.

If a local infection appears, then the blood should be pressed out and the wound treated with tincture of iodine. If there is a deep penetration of the infection, the wound should be opened by a physician so that the

disinfection can be made more thorough. If a deep abscess forms, a repeated treatment with a 3 per cent aqueous solution of phenol will usually cause it to subside.

After the end of a dissection the hands should be washed with soap and rinsed with 60 per cent alcohol or a 1 per cent solution of mercuric chloride. Also beneficial are the proprietary ointments used by surgeons.

The danger of infection from the preliminary dissection can be reduced appreciably by treating the temporal bone for a day with 5 per cent Formalin solution (*i.e.*, 5 volumes of the commercial 40 per cent solution of formaldehyde to 95 volumes of water). Often the finer dissections are hampered by the effects of formaldehyde gas on the eyes, and a solution of benzalkonium chloride (Zephiran chloride) is better. However, these solutions produce a considerable hardening of the tissues.

General Preparatory Methods. The fresh temporal bone is held in a certain position by being embedded in plaster in a heavy metal box as

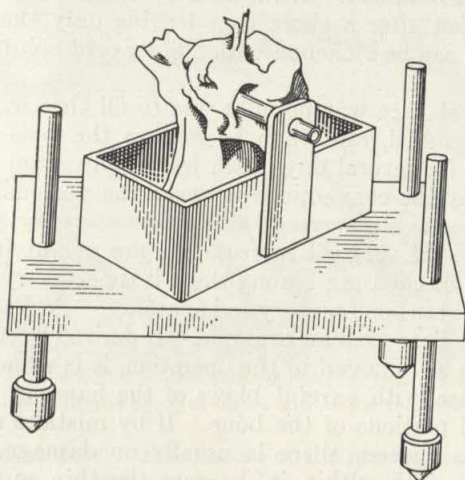


FIG. 3-1. A box for embedding a temporal bone in plaster.

shown in Fig. 3-1. The portions of the surface that are not to be dissected are covered with thin plaster, so that only a few drill holes are left free to work through. In this way a direct contact with the specimen is avoided. The metal holder can be fitted with a strong clamp with which to attach the specimen to the measuring equipment. As in many experiments it becomes necessary to introduce aerial sounds into the external auditory meatus, a tube is fastened to the box so as to extend to the meatus. To make it easier to remove the specimen at the end of the experiments, an equal volume of siliceous earth may be added to the plaster.

Zinc oxyphosphate cement as used by dentists is best for fastening a tube into the external meatus or sealing glass windows over openings. It sticks very well to fresh bone if surplus fluid is removed, even though the surface is not entirely dry.



The simplest way to prepare a permanent specimen is as follows. The temporal bone is kept for 48 hr in a 10 per cent Formalin solution, and then, after it is taken out, the excess fluid is sucked away and the specimen dried in the air. If the soft tissues have been removed properly, this treatment gives a good specimen.

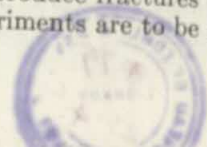
If it is desired to cut the hard temporal bone with a knife it is necessary to decalcify it with 5 per cent nitric acid. If this solution is changed daily, an adult bone will be decalcified in 3 or 4 weeks. It is then kept in 10 per cent Formalin for 48 hr, washed in running water for 24 hr, and finally preserved in 80 per cent alcohol.

If the soft tissues are to be removed from the bones by maceration, a 5 per cent solution of potassium hydroxide is used and changed daily for the first few days. The eardrum resists maceration better than other tissues, and may be left after the others are dissolved away if the time is properly chosen. If a portion of the eardrum is cut away, a good view of the middle ear is obtained. If the fluid is warmed to 60°C, the auditory ossicles will fall out after a short time leaving only the temporal bone itself. The bone can be bleached with a 6 per cent solution of hydrogen peroxide.

A procedure that once was popular was to fill the cavity of the inner ear with Wood's metal, and then to remove the bones altogether by macerating them for several days with warm potassium hydroxide solution. In this way the connections between the various cavities can be made out.

A large number of surgical instruments are useful for work on the temporal bone. In choosing among them it is necessary to bear in mind the difference between bone surgery and anatomy. Perhaps this difference can best be made clear with an example. If desired portions of the temporal bone are to be removed in the operation, it is usually best to use a chisel. In its use with careful blows of the hammer it is possible to splinter off small portions of the bone. If by mistake one of the semi-circular canals is opened, there is usually no damage to the delicate membranous labyrinth within it, because the thin mucous membrane enclosing this structure yields readily and is not cut by the chisel. The opening will later be closed by healing processes, and the sense of equilibrium will not be lost. On the other hand, if a dental burr is used, an accidental entrance into the canal can have a serious result. The rapid motion of the burr and the accompanying bone dust will often destroy the membranous labyrinth. In many anatomical preparations this is of no serious concern, and here it is better to use drills and saws because they give more exact results than the chisel. A small specimen in particular is difficult to hold in the plaster cast in a position corresponding to the one familiar to the surgeon when operating on a living person, and so the use of a chisel is often more awkward for the anatomist than for the surgeon.

Bone forceps are more useful than the chisel for rapid exposure of the middle ear, but they often produce fractures of the bone and should not be employed if critical experiments are to be made.



The most commonly used instruments are pictured in Fig. 3-2. The sharp-edged curette is used to scrape the surface of the bone. The injection needle is connected to an air pump and used to suck away excess fluid and bone dust. Also serviceable are a number of glass threads tipped with little spheres, which can be applied to the ossicles to test their mobility. Such threads when pushed against a surface with increasing force will exert a pressure that rises to a maximum and then maintains this maximum value as the force is further increased. The instruments ought not to be too small, or progress will be slow and the work will be fatiguing. An otolaryngological mirror will give adequate illumination. A small nickel-plated vise is often useful in sawing.

If the structures of the cochlear lumen are to be investigated it is necessary to use a magnification of thirty to seventy times. A wide-field binocular microscope giving this amount of magnification will cover an

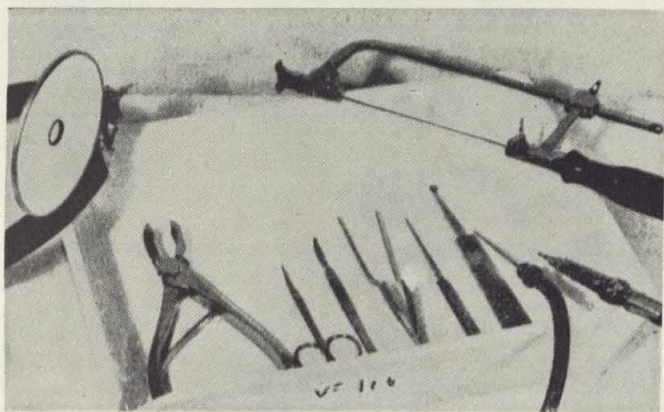


FIG. 3-2. Instruments used for dissection of the temporal bone.

area 6 to 3 mm in diameter. The success of the preparation depends upon the speed and accuracy with which various instruments can be brought into this field of view, for a single mistake can nullify all that has gone before. Therefore the handles of all the instruments need to be standardized and various supports provided for finger and hand. Then, after a sufficient amount of practice, a person can position the point of an instrument within 1 mm without looking at it.

In order that instruments may always be gripped in the same way, it is best to make the handles three-sided and to equip them with a projection that acts as a rest for the forefinger. A drill that was constructed in this way is shown in Fig. 3-3. If the operator's fingernail is of the correct length, the distance between his forefinger and the point of the instrument is then fixed. Similar handles have been made for a variety of instruments, including needles, hair probes, scalpels, brushes, and the like. Some of these were fitted into interchangeable chucks, and others had handles molded from sealing wax or a similar substance.

It is important that the arm be positioned in a comfortable way. The

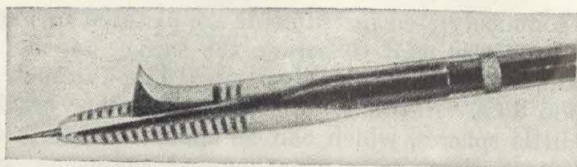


FIG. 3-3. A drill designed for uniform gripping.

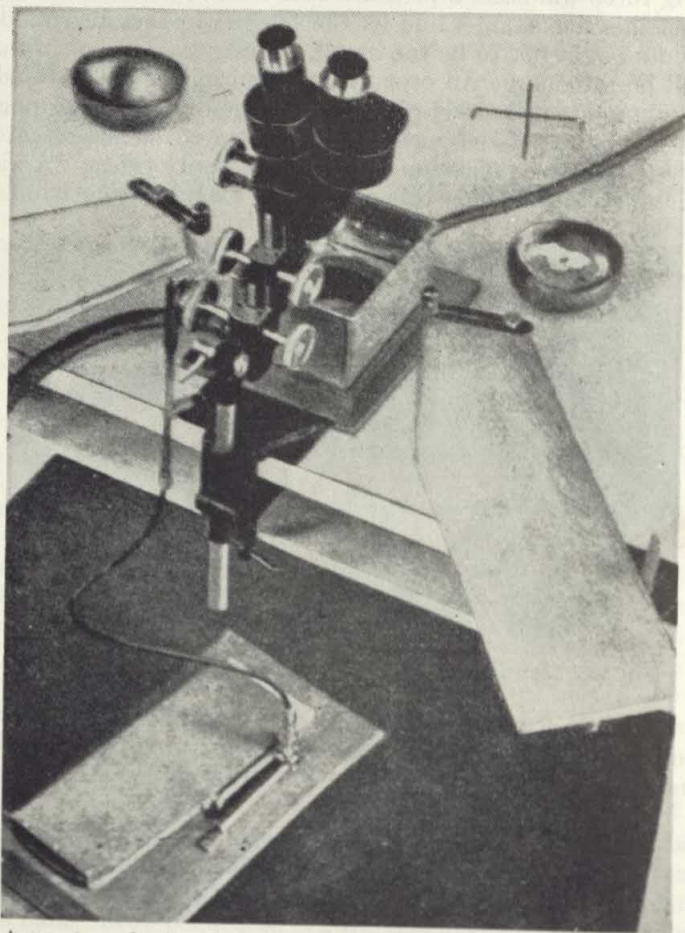


FIG. 3-4. Armrests and microscope for use in dissection. Focusing of the microscope may be done with the foot.

operator should hold the point of an instrument in the visual field of the microscope, and then set the armrests, as indicated in Fig. 3-4. The armrests shown have a metal cylinder about 2 cm in diameter placed so that the little finger can curl around it, thus determining the position of the wrist. Also a crossbar near the lower end of the board serves to locate the elbow. Additional points of support are undesirable because the arm tires if held too rigidly in one position.

To keep both hands free for dissecting, a lever that can be moved with the elbow or a pedal that can be operated with the foot may be used to adjust the microscope, as described in Chap. 4, page 36.

Preparation of the Cochlea. In the following paragraphs will be described in detail the procedures employed by the writer in preparing the cochlea for detailed measurements.

To estimate the position of the cochlea within the petrous bone, it is best to begin at the inner surface adjacent to the brain and to follow the auditory nerve. For this purpose, the canal carrying the auditory nerve is suitably enlarged by the drill until the nerve can be seen clearly in the cochlear axis. The axis may be identified by its direction. The petrous

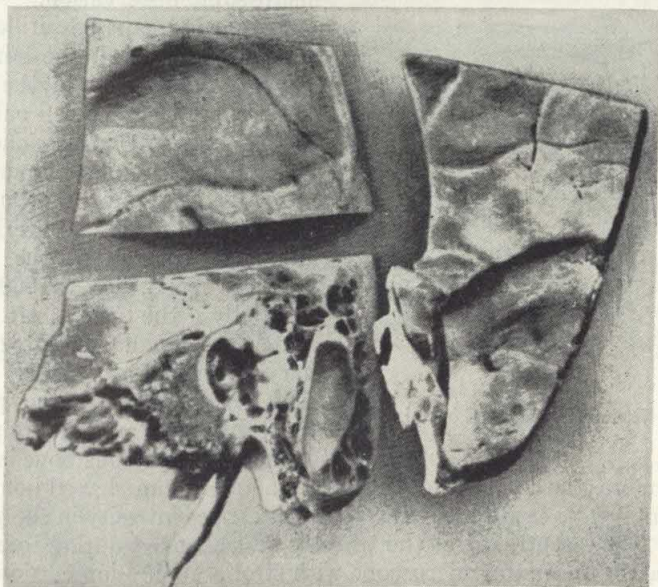


FIG. 3-5. Preliminary dissection of the temporal bone.

bone is then sawed in two with a fret saw in a direction perpendicular to the cochlear axis, as shown by the vertical cut in Fig. 3-5. A second, horizontal cut removes the superfluous part of the skull.

Thereafter, the section of bone containing the cochlea is cemented into an exactly hemispherical iron shell, 9 cm in diameter, in such a way that the center of the cochlea coincides with the center of the hemisphere. (The wire cross visible in Fig. 3-4 facilitates the orientation when it is set on the hemisphere.) The cement used is a mixture of equal parts of gypsum and siliceous earth, which can be removed more easily later on than gypsum alone, and the bone is covered with this mixture except in the immediate vicinity of the cochlea. The hemisphere is set in a circular opening, 7 cm in diameter, in the floor of the box shown in Fig. 3-4. In this opening the hemisphere together with the specimen can now be turned into whatever position is desired under the microscope. The

floor of the box is a steel plate, ground smooth, that can be shifted relative to a second, fixed plate, and this permits easy displacement of the specimen in the horizontal plane. If the contact surfaces of the two plates are lubricated by viscous grease, the extent of displacement can easily be controlled by varying the time during which a continuous pressure of the fingers is applied to the upper plate.

To avoid damage to the fine cochlear tissues by capillary forces, the cochlea should be prepared under water. A physiological saline solution is therefore kept flowing constantly through the container. The speed of flow is adjusted to carry away most of the bone dust from the drilling, without allowing waves to form on the surface of the liquid to disturb microscopic observation.

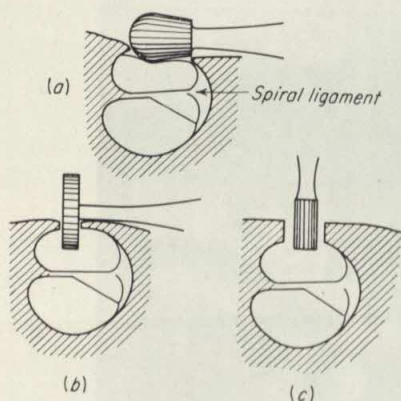


FIG. 3-6. Various methods of opening the cochlea.

Furthermore, the center of the cochlea is a mushroom-shaped bony structure that breaks easily if there is the slightest eccentricity in the grinding wheel. The eccentricity of the wheel is best checked during rotation by examination under the microscope with stroboscopic illumination.

The greatest difficulty in opening a cochlear canal is that it is lined with a tough, thin membrane that adheres only loosely to the bone. Therefore, if the drill is used at the most convenient angle, at a tangent to the canal (as in Fig. 3-6a), bone fragments detach themselves from the membrane while the latter is pushed inward. A considerable part of the membrane then usually pulls away from the bony wall, so that the spiral ligament (and with it the basilar membrane) also loses its hold on the wall.

For this reason, the first step taken in opening the canal is to grind away all the bone parallel to the basilar membrane until only a small part of the wall—a few tenths of a millimeter—remains. This operation is easy with a little care, because the bone appears white when it is thick and bluish gray when it is thin. With only the color as a guide, therefore, the thickness of the wall can be reduced along the curved canal, which becomes visible through the bone as a dark strip. After this preliminary work, a flat-headed grinding wheel is used to cut along the center of the

The bone can be drilled and ground with ease if the bone dust stays in suspension in the water. The dust is then carried out of the field of observation in clouds with the stream of liquid. To make the bone dust fine enough, a burr with fine teeth (a finishing burr) is used, and it is rotated at the highest possible speed, up to 8000 rpm, especially if the bone is soft. Even better are small emery wheels of varying fineness, especially for the final work. The grinding pressure must be kept as light as possible because the petrous bone is fragile.

canal, as shown in Fig. 3-6*b*, and to open a slit over its entire length. As the shaft of the wheel lies on the bone surface previously prepared, this operation is safe with a grinding wheel of proper size. Extensive loosening of the membrane from the bony wall occurs rarely under these circumstances, because the wheel's direction of rotation is made such that the grinding starts from the inner part of the canal and proceeds outward. Thus the lining is pressed against the wall and does not separate from it. In opening the canal, it is well to begin near the cochlear axis and to work gradually toward the outer edge. In the approach shown in Fig. 3-6*b*, the initial opening is made above the bony section of the partition by means of a wheel-shaped drill about 0.6 mm in diameter, rotating clockwise and with its axis of rotation placed at right angles to the canal. After the exact orientation is obtained, the grinding proceeds longitudinally along the canal. Care is especially important when the grinding begins at the apex, because Reissner's membrane is easily injured there.

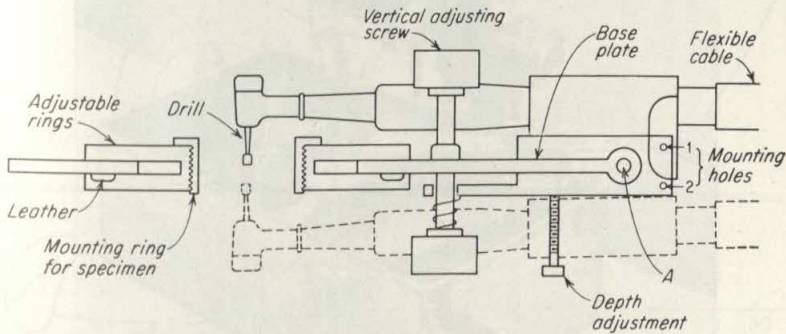


FIG. 3-7. A mechanism for opening the cochlea on both sides of the basilar membrane.

With sufficient practice the technique of drilling can be developed to the point where the bone does not chip off and all the ground surfaces are clean.

Another way to prevent separation of the membranous lining from the bone is to use a cylindrical grindstone that is guided along the scala tympani as in Fig. 3-6*c*. This proved to be difficult as a freehand operation, so that the apparatus illustrated in Fig. 3-7 was used.

The device is supported on a base plate with a circular opening. On either side of the plate are two flat rings screwed to each other and capable of adjustment in the circular opening. The mounting ring containing the specimen is screwed into the center of one of the flat rings. At the back edge of the base plate is mounted a brass block that can be moved around an axis *A*, and whose angle with the base plate is regulated by the height-adjusting screw. Attached to this first block by means of two tabs and a pin is a second brass block that holds the dental drill. The pin acts as a hinge so that the drill can be raised out of its normal setting at any time to examine the spot being drilled. If the pin is removed and reinserted in hole No. 2, the drill can be shifted to a position, indicated by the dotted lines in Fig. 3-7, which is the mirror image of its

previous one. This allows the specimen to be drilled from below at a spot exactly corresponding to the previous point. The difference in height between the two drill positions is adjusted by a small screw on the brass block, and the residual thickness of the specimen can be determined in the same operation. This method makes it easy to open the canals on both sides of the basilar membrane. For this operation the petrous bones are cemented with gypsum into the interchangeable mounting rings to be seen in Fig. 3-7. For drilling from below, the base plate is turned over.

Because the work had to be done under water, the entire apparatus was set diagonally into a water bath and in this way was brought under the microscope. Figure 3-8 is a photograph of the bath. The base

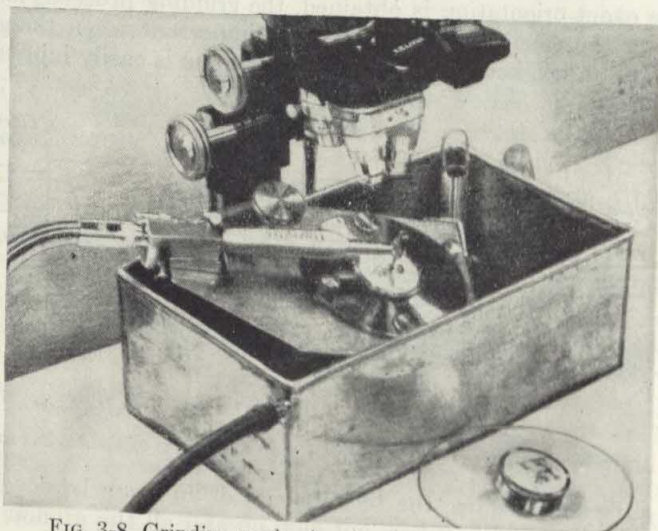


FIG. 3-8. Grinding mechanism in place in a water bath.

plate is set on supports so designed that the plate can be turned under water. In the far corner of the bath is the adjustable discharge tube, which permits regulation of the depth of the liquid. In the glass dish shown outside the bath can be seen one of the mounting rings with a second petrous bone cemented into it. For further dissection, the metal rings can also be screwed into the hemisphere shown in Fig. 3-4 with the help of an adapter.

After a measurement has been made at some spot on the basilar membrane, the exact location of the spot in the sharply curved cochlea is still a special problem. To solve this problem a number of cochleae were opened at the apex and various points along the basilar membrane were plotted with the help of a camera lucida. Each point plotted represented the center of the most pliable part of the membrane. As each section was plotted, the entire cochlea was gradually leveled and the projection of the entire membrane on a plane perpendicular to the cochlear axis was determined. Figure 3-9 shows the average

curve obtained, including the outer edge of the stapes and the middle of the helicotrema, the latter indicated by a circle.

If a measurement is made of the vertical pitch of the several turns from cross sections of the cochlea, it becomes apparent that the membrane, because of this pitch, is at most only 2 to 3 per cent longer than its projection. Therefore, in Fig. 3-9, the length of the curve is also measured and entered. The edge of the stapes is taken as zero. From this point, the basilar membrane dips sharply below the plane of the drawing, so that it appears shortened and would protrude about 1 mm beyond the edge of the stapes if it were straightened out. The physical relationships in this area can be grasped only with difficulty, so that the length of the vibrating column of liquid also cannot be measured with great

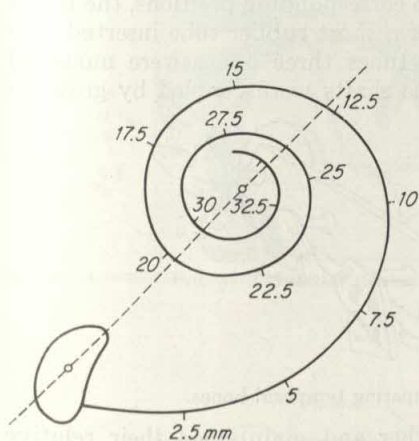


FIG. 3-9. Form and length of the basilar membrane in man. Distances are measured from the stapes in millimeters.

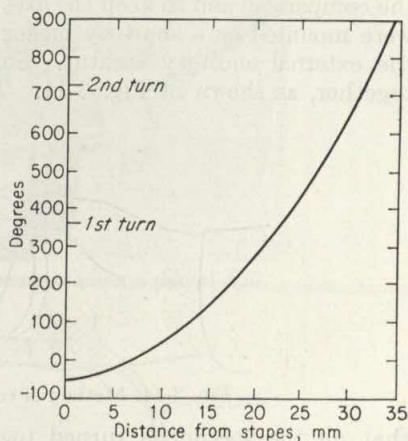


FIG. 3-10. The relation between the direction of a tangent to the basilar membrane and distance from the stapes.

accuracy. The average length of the human basilar membrane is 35 mm in all, taking into account its flexion near the stapes.

By comparing a particular specimen with this chart, it was possible to fix positions in the specimen, especially when the stapes and the helicotrema were visible. Sometimes the camera lucida was used in this operation. In other experiments only a small section of the canal was opened, and only the direction of the canal was known. In this case, the direction of the canal is referred to a straight line drawn between the helicotrema and the center of the stapes. The angle between these two directions is measured under the microscope by substituting for the usual eyepiece one carrying a cross hair that can be rotated about a circular scale graduated in degrees. From this angle the distance of the exposed section from the edge of the stapes can be calculated from the graph in Fig. 3-10. This graph was obtained by measuring the directions of tangents to the curve in Fig. 3-9. In most cases, it is sufficient to bring the chart into the same position as the specimen and to read the distance of the point in question from the stapes directly from the

numbers on the chart. The chart is for a right ear as seen from the apex, and a mirror image of the chart serves for the other ear or direction of regard.

Many of the experiments to be described in later chapters required the drilling of holes in the temporal bone. Because individual temporal bones differ greatly from one another, it is difficult to drill into the bone from the outside to reach a particular point. A method was developed to aid in this orientation. A collection was made including bones of a great variety of sizes and shapes, from which one could usually be selected to match a specimen that was to be prepared. The reference bone was opened to disclose the structures of interest, and the new specimen (which could not be dissected in this way) was compared with it. To facilitate the comparison and to keep the axes in corresponding positions, the bones were mounted on a shaft by means of a short rubber tube inserted into the external auditory meatus. Sometimes three bones were mounted together, as shown in Fig. 3-11. The shafts were coupled by gears so



Fig. 3-11. Method of comparing temporal bones.

that all the specimens turned together and maintained their relative positions.

Experiments concerned with the movements of the eardrum and ossicular chain often required the making of an opening into the external auditory meatus or the middle-ear cavity. It was important that these openings be made quickly to prevent undue drying of the eardrum. Also, there are only a few places where such openings can be made without damage to the various ligaments that hold the ossicular chain.

A simple drilling device is shown in Fig. 3-12. It consists principally of a pointer and a dental drill that works in a guide tube. The drill can be oriented in a particular direction, and a stop is provided to give it a certain maximum depth from the pointer. If, for example, the middle ear is to be opened, the drill is set at a distance of 1 mm from the pointer. The end of the pointer is then located at the middle of the eardrum and to the left and superior to the manubrium of the malleus. The specimen is held in this position while the rectangular trough shown in Fig. 3-12 is placed over it, and plaster is used to fix it firmly in position. After the plaster has hardened, the pointer is removed, and the drill is used to open a hole to the desired depth.

The drilling is done with a special burr so as to keep the drilling pressure low, and then the opening is widened with a milling cutter. Because

there are no ossicles in the lower half of the tympanic cavity, this opening of the middle ear does not do any damage.

A more effective drilling device consisted of a pair of calipers, with one arm stationary and the other free to rotate. A wire pointer was connected to the end of the fixed arm, and a dental drill was connected to the

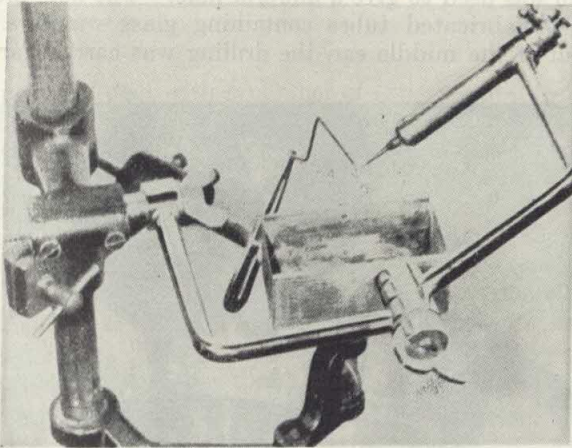


FIG. 3-12. Pointer device for positioning a dental drill.

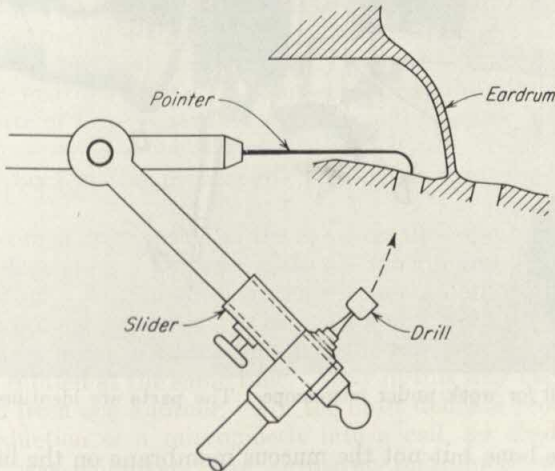


FIG. 3-13. Caliper device for drilling.

rotating arm. The drill was placed so that when the two arms of the calipers were moved together the pointer fitted into the center of the drill tip.

To make an opening at a desired place, as for example at a point in the wall of the external meatus, the specimen was fixed in a holder and the pointer set on the spot where the hole was to be made, as shown in Fig. 3-13. A stop was set to determine the depth of drilling, and the arms

of the calipers were brought together as far as they would go. Sometimes the drill was shut off automatically by means of a switch that was actuated when the stop was reached.

When openings were made for the placing of glass windows through which movements of the middle-ear mechanism could be observed, a standard drill was used to give a uniform hole. The hole then could be sealed with prefabricated tubes containing glass windows. To keep bone dust out of the middle ear, the drilling was carried far enough to

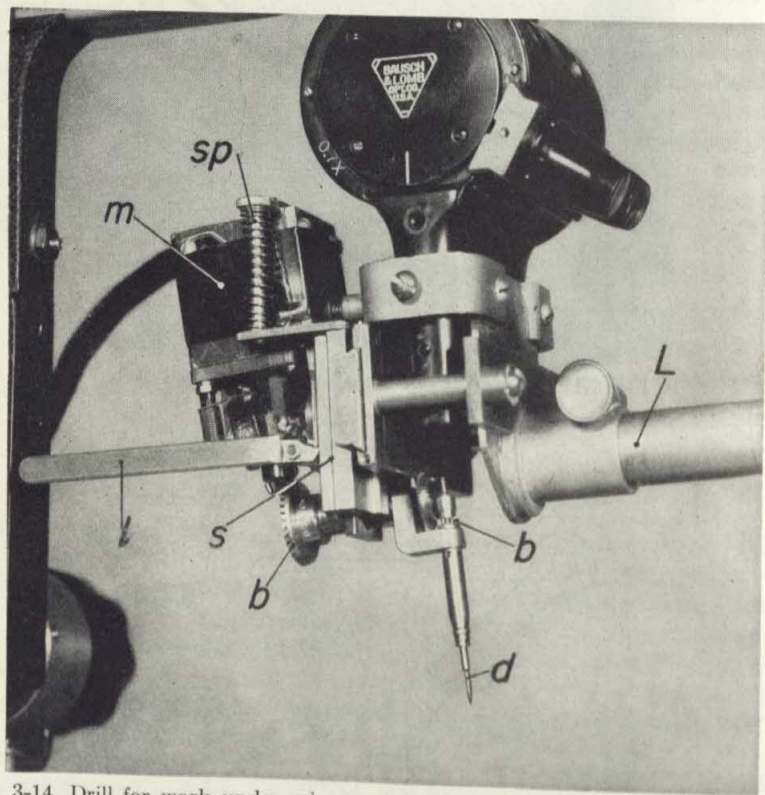


FIG. 3-14. Drill for work under microscope. The parts are identified in the text.

penetrate the bone but not the mucous membrane on the inner surface. If a tube with a serrated edge was used as the drill, the bone could be removed as a plug, and the membrane could be cut out with a knife.

When it was necessary to make microscopic openings in the wall of the cochlea, a special drill was used and mounted on the dissecting microscope, as shown in Fig. 3-14. The axis of the drill *d* was located midway between the two objectives, and the drill was driven by the motor *m* and two bevel gears *b*. The whole assembly could be moved vertically in the slide *s* by means of a lever *l*. Its weight was balanced by a spring *sp*. *L* is part of an illuminating device.

CHAPTER 4

EXPERIMENTAL APPARATUS AND METHODS

This chapter will deal with a number of experimental techniques that were developed for the examination and measurement of the vibratory movements of auditory structures.

A problem of first importance is illumination. Many of the sensory structures of the labyrinth of a living animal are nearly transparent and immersed in fluid. With ordinary diffuse light little can be seen. In this situation a slit lamp can be used with the same success already well realized in the examination of the eye. A narrow beam of light brings out the boundaries of the cells so that small displacements of the cells can be observed.

Another problem has to do with the microscope. Lateral displacements can easily be observed, but displacements along the axis of view are difficult to evaluate even with a stereoscopic microscope. To meet this problem a microscope was constructed in which the third dimension was exaggerated. This instrument proved to be particularly useful in observing the perforation of a thin membrane by an electrode.

Vibratory movements are most readily observed by means of a stroboscope. This instrument can be adjusted so that the vibrations seem to occur at a rate of 1 cps regardless of the actual vibratory rates. Also, a special form of stroboscope has been designed to give measurements of phase differences in the movements of different parts of the auditory mechanism.

For the surgical preparation of the ear three different types of manipulators were developed. For preliminary surgical exposures a finger rest was satisfactory. For finer dissections a micromanipulator with four degrees of freedom was used. This instrument permitted the making of carving movements in which the tip of the tool was not only displaced in space but rotated at the same time. Only in this way may membranes be separated from one another. For the most delicate procedures, such as the introduction of a micropipette into a cell, an air-driven micromanipulator was employed. An air-driven instrument was necessary because any manual contact with the preparation produced intolerable disturbances.

It was desirable for theoretical reasons to obtain numerical values for the impedance of the basilar membrane. For this purpose a test needle was made that could record forces as small as 1 dyne. It was mounted on the objective of a microscope and was moved into contact with the tissues by means of the focusing screw. Its first contact with the basilar membrane was observed on the screen of an oscilloscope. Then the needle was moved down 1 μ farther, and a measurement was made of the

resulting increase in pressure on the tip of the needle. The ratio between the pressure increase and the movement gives the mechanical impedance for this deformation. It was easy to prove that the elasticity of the basilar membrane of a guinea pig did not change when the guinea pig was killed, and that it remained within a few per cent of its normal value for several hours after death.

This constancy in mechanical properties was not found for the eardrum. If no precautions are taken this membrane dries out in a few hours after death and its stiffness increases.

A capacitive pickup was used to measure the vibration of various parts of the ear. This instrument was made small enough to record the vibrations of the different regions of the eardrum.

Special problems arose in the study of hearing for tones below 10 cps. In this region, the ear's sensitivity increases so rapidly with the frequency that overtones are particularly disturbing. After many failures to produce suitable electric filters, a simple mechanical filter was developed. This filter consisted of a horizontal glass tube containing a few drops of mercury at appropriate intervals.

By the use of automatic anatomical techniques it was often possible to make a preparation of the temporal bone in as little as 10 min, but it always took a long time to make measurements for a series of many individual frequencies, and during this time numerous changes could occur. Therefore the shock method was used, in which the transients of the system were measured on

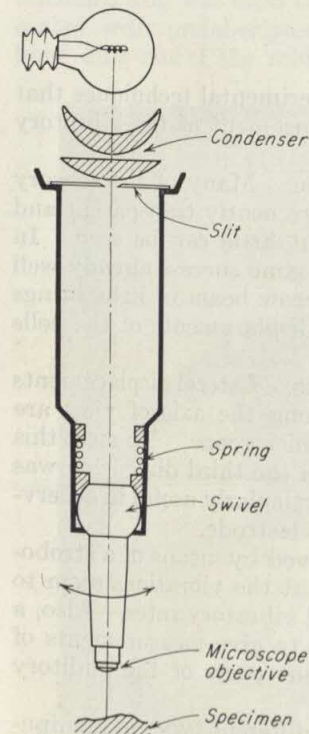


FIG. 4-1. Design for a slit lamp.

stimulating with a sharp click. From the nature of these transients the response of the system to sinusoidal vibrations can be calculated. This method later proved to be useful also in the study of bridges. It is usually impractical to construct a mechanical oscillator with sufficient energy to set a bridge into sinusoidal vibrations at different frequencies, but it is easy to set off a small charge of explosive near the bridge and to measure its transient responses.

These various instruments and procedures will now be described in detail.

THE SLIT LAMP*

The cochlear partition of a living animal is almost wholly transparent, so that only the bony parts of the wall are visible when diffuse illumination or a broad beam of light is used. Much more suitable is the slit lamp

* Extract from Art. 67 as listed in the Author's Bibliography. Published in 1953.

shown in Fig. 4-1, which is similar to the type introduced into ophthalmology by Gullstrand. The image of the filament of an incandescent lamp is projected by a condenser in the plane of a microscope objective in order to provide a high light intensity. The microscope objective projects the slit onto the object. A flat beam of light, about 0.005 mm thick, is satisfactory.

Although the problem of illumination is similar, the fact that the white bony walls of the cochlea reflect light makes observations of the cochlea more difficult than observations of the eye. The outline of the image can sometimes be made more distinct by the use of a vital stain. For a general view of the partition, it is best to concentrate the light beam on the thin bony wall, thus providing diffuse illumination in the canals from the inside. It is convenient to mount the microscope objective on a swivel so that the beam can be directed to the best position by a delicate movement of the finger tips.

A Leitz water-immersion objective with a magnification of seven times was often used as the projection lens.

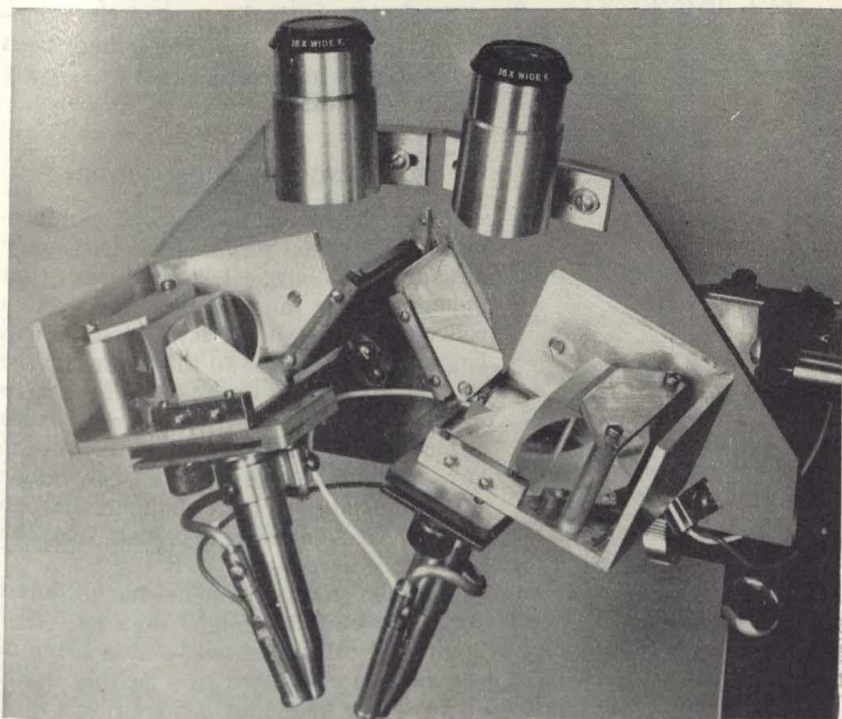


FIG. 4-2. A stereoscopic microscope with exaggerated depth. The cover was removed to show the arrangement of the prisms.

A MICROSCOPE WITH EXAGGERATED DEPTH*

It is difficult to judge the exact position of the tip of a micropipette inside the organ of Corti because the translucent structure does not give

* Not previously published.

suitable points of reference. An improvement in the third dimension provided by a stereoscopic microscope can be obtained by increasing the angle between the two objectives. This angle can be made about twice as large as the normal angle of view, and after a certain amount of training the images can be fused. The arrangement is shown in Fig. 4-2. As indicated, prisms and mirrors are used to keep the image about 25 cm from the oculars. Screws are provided on the tops of the objectives to permit a proper adjustment of the relative position of the images in both horizontal directions. A small light is mounted on each objective and adjusted so that the two images are about equally bright.

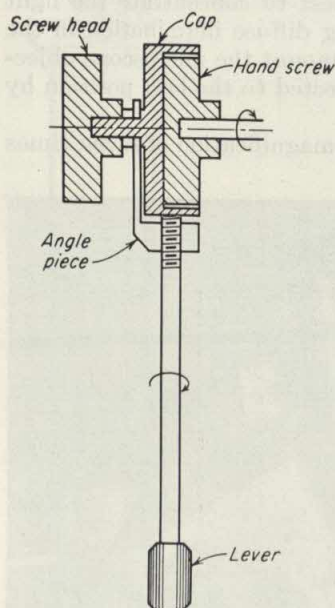


FIG. 4-3. Manner of fitting a lever to the focusing screw of the microscope.

and makes a connection to the lever. A screwhead is used to lock the angle piece in any desired position on the cap.

This lever can easily be moved with the elbow. A somewhat different device was designed to permit focusing by movements of the foot. For this purpose the microscope is equipped with a rack-and-pinion drive in addition to the usual one, and its knob is connected to a flexible shaft. The other end of this shaft leads to a spur gear that is driven by a rack attached to a treadle. The microscope is partly supported on a compression spring contained in a tube, so as to reduce its weight and give a smooth movement. These arrangements are advantageous, not only because they reduce fatigue, but also because they leave both hands free for the surgical dissections.

* Extract from Art. 61 as listed in the Author's Bibliography. Published in 1951.

This system produces a noticeable increase in the sensation of depth. The height of the organ of Corti seems much increased, so that the position of an electrode tip relative to the cells can be observed more precisely. In some instances, this instrument provided the only means of determining whether one of the membranes of the organ of Corti had been penetrated by an electrode that was slowly moved downward.

FOCUSING THE MICROSCOPE*

Use of the focusing screw of the microscope in the usual way becomes extremely fatiguing in surgical procedures that require 2 hr or more to carry out. As a convenient accessory, a lever about 30 cm long can be attached to this screw in the manner shown in Fig. 4-3. The cap is pressed over the knurled hand screw with a thin piece of leather between to prevent any marring of the finish. An angle piece is fitted to a short shaft on the cap

STROBOSCOPIC ILLUMINATION*

The observation of a periodically moving object (such as one of the auditory ossicles or some part of the inner ear) is greatly facilitated by the use of a stroboscope. It is most convenient if the flashes of illumination are given a frequency that differs from the frequency of the motion by 1 cps, for then the object will seem to vibrate at this difference frequency and its movements can be studied in detail.

With most stroboscopes the frequency is not stable and the observed motion is varying, so that frequent readjustments of the stroboscopic frequency are required. To avoid such adjustments, an arrangement was set up for automatic maintenance of the stroboscopic frequency at a constant difference (say, 1 cps) from the frequency of the object under examination. With this arrangement it is possible to make continuous

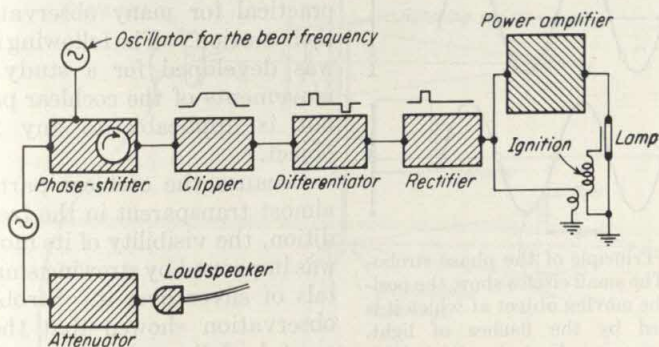


FIG. 4-4. Schematic circuit for the automatic stroboscope.

observations of an object while its frequency of vibration is swept through a broad range.

The circuit arrangement for obtaining this result is shown in Fig. 4-4. A master oscillator is connected through an attenuator to a loudspeaker (or vibrator) leading to the animal's ear. The same oscillator is connected to a phase shifter, and then to a clipper that distorts the sinusoidal voltage into a trapezoid. This wave is then differentiated, producing two rectangular pulses. The length of these pulses can be altered by varying the amplitude of the sinusoidal voltage fed to the clipper. A rectifier then removes one of the pulses, and the remaining one is amplified to 2000 volts and fed into a high-pressure mercury-arc lamp. To ignite the lamp, the rectifier pulse is amplified separately and led into a shock coil to produce a sharp spike on a free-ending wire near the wall of the mercury lamp. This spike is given a voltage of the order of 15,000 volts, and it triggers even old lamps. The intensity of the light can be adjusted by changing the length of the pulses, but in general the length of the duty cycle is kept at 2 to 5 per cent. Such a short duty cycle is necessary to give a sharp stroboscopic picture.

The stroboscope was used in the frequency range from 10 to 2000 cps.

* Extract from Art. 67.

Within this range it was possible to make satisfactory observations of the organ of Corti. The phase shifter covered 360° , and its settings were independent of frequency. Its dial was rotated by a low-frequency oscillator, and if given a rotation of 1 per sec (360° per sec) the object would seem to move at this rate, regardless of the actual driving frequency.

The master oscillator could be swept through a broad frequency range in a few seconds, and so the behavior of a vibrating system could be quickly scanned.

THE PHASE-MEASURING STROBOSCOPE*

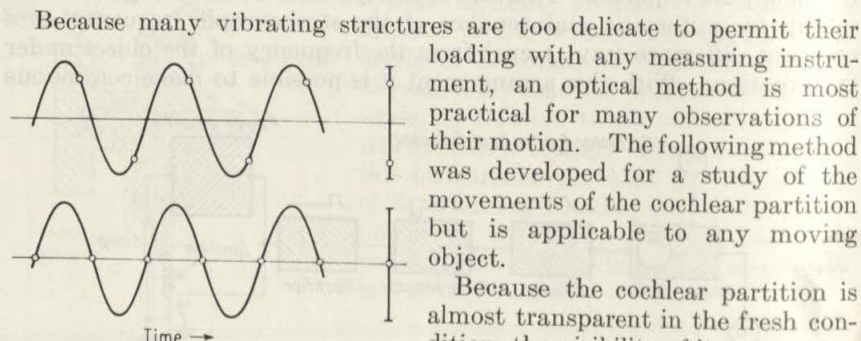


FIG. 4-5. Principle of the phase stroboscope. The small circles show the positions of the moving object at which it is illuminated by the flashes of light. What is seen is indicated on the right. In the upper sketch, two spots of light are seen. In the lower sketch, the phase of the flashes has been adjusted so that only one spot is seen.

Because many vibrating structures are too delicate to permit their loading with any measuring instrument, an optical method is most practical for many observations of their motion. The following method was developed for a study of the movements of the cochlear partition but is applicable to any moving object.

Because the cochlear partition is almost transparent in the fresh condition, the visibility of its movement was improved by strewing small crystals of silver over it. Stroboscopic observation showed that these flat crystals follow the movements exactly up to the highest frequencies investigated. With proper illumination of the partition, the observer sees a large number of bright, shiny

dots that spread out into a band when the basilar membrane is set into vibration. For accuracy of the measurements the silver crystals may be made so small that even when enlarged over a hundred times they appear as sharp dots.

If now the vibrating cochlear partition is illuminated by a regular series of light flashes whose frequency is twice that of the frequency of vibration, each point will appear doubled, as indicated in Fig. 4-5. The distance between the points will depend upon the phase angle between the vibration of the membrane and the series of flashes. The separation becomes zero, as the lower drawing shows, if the vibrating point is illuminated just as it passes through the zero position.

The equipment can be utilized to determine the phase relations between two vibratory structures. In a particular application it was used to measure the phase difference between the movements of the stapes and the resulting movements of the basilar membrane. For this purpose both a sinusoidal alternating current and a series of light flashes

* Extract from Art. 47 as listed in the Author's Bibliography. Published in 1947.

of doubled frequency were produced by the same stroboscopic disk. The alternating current was used to activate an electrodynamic vibrator that drove the system under observation (in this example, the stapes). Then a phase-shifting device was adjusted so that the bright dots on the stapes were in coincidence. Finally the basilar membrane was observed and the phase angle was changed until this membrane also was always illuminated in its zero position. The difference between the two phase settings represents the phase difference between the movements of the two coupled structures, the stapes and the basilar membrane.

Details of the photoelectric siren are shown in Fig. 4-6 (Schouten). A source of light L_1 gives uniform illumination of a large condenser lens. Immediately in front of this lens (and between it and the light) is a

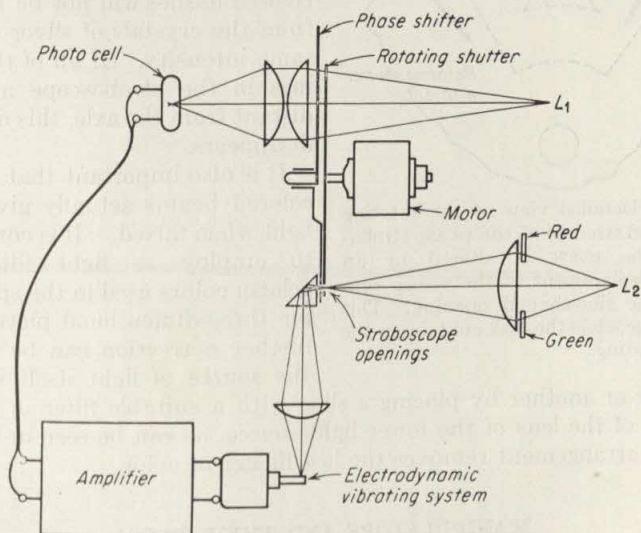


FIG. 4-6. Arrangement of the phase stroboscope.

screen with a sine-shaped opening, and in front of this opening is a rotating stroboscopic shutter. The shutter has a very narrow slit so placed that, as it moves past the opening, the amount of light striking the condenser lens undergoes a precise sinusoidal variation about its average value. The condenser lens concentrates the light that passes through it upon a photocell, which activates in turn, through an amplifier, the electrodynamic vibrating system. In order to change the phase of the generated alternating current the screen with the sinusoidal opening can be turned about the axis of the rotating shutter as shown in Fig. 4-7. The angle between two adjacent slits in the shutter corresponds to a phase shift of 2π radians.

The rotating shutter has near its edge some small holes that control the stroboscopic illumination supplied by L_2 . For convenience the light beam is directed by means of a totally reflecting prism and is concentrated on the preparation with a condenser lens. The exact observation of the

coincidence of the two bright dots is made much easier if the successive flashes, instead of being white light, are alternately red and green. Then the membrane will usually glisten with spots of red and green light, which with proper phase setting will add up to white. The exact phase setting can be found at which the bright points of light are no longer fringed with color.

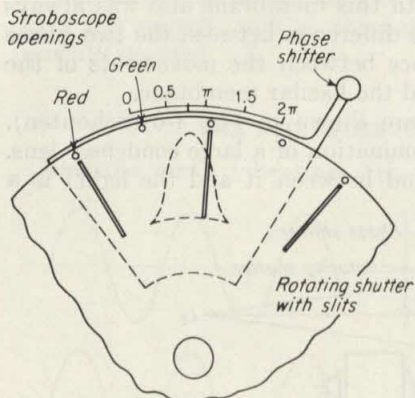


FIG. 4-7. Detailed view of the rotating shutter and window of the phase stroboscope. The phase is altered by an angular displacement of the screen containing the sine-shaped opening. This can be done while the disk containing the slits is rotating.

In the use of the apparatus, certain precautions are necessary. There must be no change in the direction of the light beam when the color changes. Otherwise it can easily happen that the two colored flashes will not be reflected from the crystals of silver with the same intensity. If all of the openings in the stroboscope are equidistant from the axle, this difficulty disappears.

It is also important that the two colored beams actually give white light when mixed. It is convenient to employ as light filters the gelatin colors used in the spectacles for three-dimensional pictures. A further correction can be made if the source of light itself is tinted

one color or another by placing a slide with a suitable filter in front of the edge of the lens of the lower light source, as can be seen in Fig. 4-6. Such an arrangement removes the last flicker of color.

MANIPULATORS AND THEIR USES*

Compared with freehand manipulation, a micromanipulator offers two advantages. First, the size of the voluntary movements of the hand is reduced, and second, the involuntary trembling of the fingers can be reduced or eliminated. As can be seen under a microscope, it is the trembling of the tips of the instruments that limits the neatness of the operations.

Preparatory Manipulator. In the sixteenth century, painting was very detailed and artists used a "painters stick" as a rest for their hands. This tool is a useful one and can be modified to increase its mobility, as shown in Fig. 4-8. The two hands rest on a platform parallel to the surface of the drawing. The left hand holds a screwdriver and the right hand a dissecting instrument. The flat surface of the screwdriver is inclined slightly, so that the point of its tip farthest to the right touches the flat horizontal supporting surface and can be used as a fixed rotating point. By rotating the screwdriver around its longitudinal axis, it

* Extract from Art. 77 as listed in the Author's Bibliography. Published in 1956.

is possible to lift or lower the tip of the dissecting tool from the flat surface in a delicate way. A lateral displacement of the left hand displaces the top of the dissecting tool laterally in the plane of the drawing. The resulting movement of the dissecting tool is reduced according to the distance between the fixed rotating point of the screwdriver

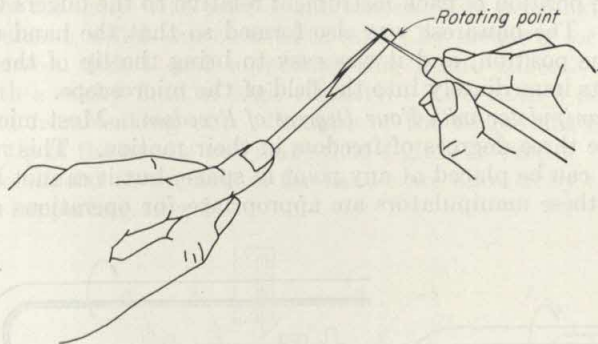


FIG. 4-8. Use of a screwdriver as an aid to freehand dissection.

and the resting point of the dissecting instrument on the screwdriver. Movements in two dimensions are obtained in this way. Movement in the third dimension is obtained by sliding the dissecting instrument along the edge of the screwdriver or displacing the right hand as a whole in the plane of the drawing. In this case the movements are again reduced by a lever action. If the dissecting instrument is a needle, a slight rotation around its axis rolls the tip along the edge of the screwdriver.

The flat handrest parallel to the surface of the drawing is adequate for preparations with a horizontal surface. For an inclined surface the setup in Fig. 4-9 is used. The object under study is placed on the left side under the microscope objectives. The handrest for the right hand is curved down and has along its edge a groove in which the screwdriver tip can be placed so that any point along the groove represents the rotating point. The left hand has a separate handrest not shown in the figure.

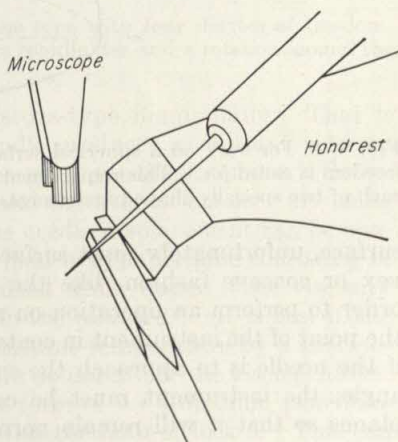


FIG. 4-9. A setup for manipulations on an inclined surface.

This last setup has been used for operations on the cochlea and the brain of guinea pigs. The stereoscopic microscope used in this work had a magnification of 150 times.

This preparatory manipulator has proved indispensable for the preliminary preparation of anatomical specimens. It has filled the difficult

gap between freehand operations and final adjustments with more complicated micromanipulators, in spite of the fact that only one hand is free to operate.

The instruments were held in a pin vise to facilitate their exchange. All the instruments and the pin vises were of exactly the same length, so that the position of each instrument relative to the fingers was always the same. The handrest was also formed so that the hand always fell in the same position, and it was easy to bring the tip of the dissecting instruments immediately into the field of the microscope.

Micromanipulator with Four Degrees of Freedom. Most micromanipulators have three degrees of freedom in their motion. This means that the needle can be placed at any point in space, but it cannot be rotated. Although these manipulators are appropriate for operations on a plane

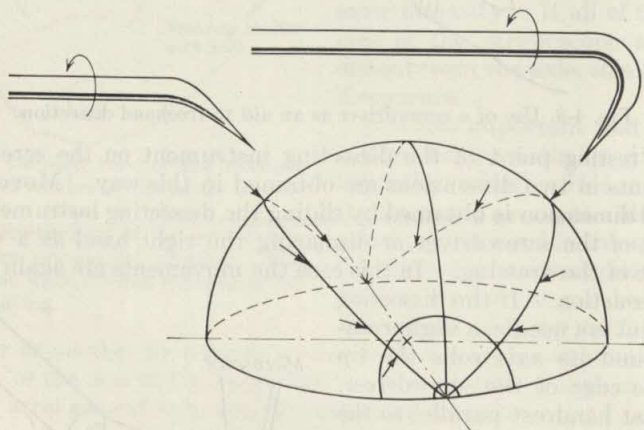


FIG. 4-10. For work on a spherical surface a micromanipulator with five degrees of freedom is called for. This requirement can be met with four degrees of freedom in each of two specially shaped instruments, one for each half of the sphere.

surface, unfortunately most surfaces of living tissues are bulged in convex or concave fashion, like the hemisphere shown in Fig. 4-10. In order to perform an operation on such a surface it is necessary to bring the point of the instrument in contact with a point on the sphere. Then, if the needle is to approach the surface of the sphere from any desired angle, the instrument must be capable of rotation in two additional planes so that it will remain normal to the surface. This means that an ideal micromanipulator should have five degrees of freedom.

Practical experience has shown that the problem can be simplified by using two differently shaped needles, one for the left (see McClung on the reflex type) and one for the right side of the sphere, thereby avoiding the rotation of the instrument in the plane of the drawing. This step allows us to accomplish our purpose with only four degrees of freedom, with a consequent simplification in the construction of the manipulator.

A micromanipulator with four degrees of freedom is shown in Fig. 4-11. It permits a displacement of the tip of the needle in three orthogonal directions, plus a rotation of the needle around the axis of the stem. The manipulator consists of a flat disk 1 gliding in a supporting ring 2. A tube 3 is inserted perpendicular to the center of the disk. A second tube 4 glides coaxially with tube 3, and contains the pencillike handle 5 of the instrument, which can be fixed to tube 4 by means of lock 6. The surfaces between disk 1 and supporting ring 2 and tubes 3 and 4 are covered with a sticky fluid of high viscosity. Two rings 8 prevent the viscous fluid from leaking out. Pressure of the finger tips on knob 7 toward the tip of the needle will make tube 4 glide in tube 3. Displacements perpendicular to the axis of the handle are allowed by the gliding of disk 1 in supporting ring 2.

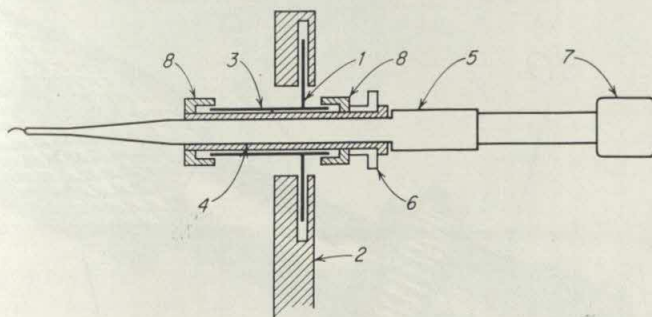


FIG. 4-11. A micromanipulator of the viscous type with four degrees of freedom. Provided are three displacements in the space coordinates and a rotation around the axis of the handle.

This micromanipulator is a pure viscous-type manipulator. That is to say, a constant pressure on the handle produces a constant velocity of motion so that the magnitude of the resultant displacement is determined by the product of the pressure and the time of action. By using fluids with high viscosity the size of the needle displacement can be controlled at a small value. The viscous fluid is flypaper glue consisting of 1 oz of castor oil and 2 oz of rosin mixed while warm. The viscosity depends upon the proportion of rosin in the mixture.* It is best if the whole microscope stand is kept at a constant temperature by a thermostat so that changes in room temperature do not affect the viscous forces.

The operating tools are made in the form of an aluminum pencillike tube 5 and are easily interchangeable with the help of lock 6. This can be done with one hand by holding knob 7 with the palm of the hand and at the same time rotating lock 6 with the forefinger and thumb. A detailed view of the lock is shown in Fig. 4-12. To fix the tool in the manipulator, pin 9 is slid into slit 10 and ring 6 is turned so that the pin is pressed against ring 8 by the spiral spring attached to ring 6.

A micromanipulator with these four degrees of freedom controlled by

* Nowadays silicone would be used, as it has a lower temperature coefficient of viscosity.

cinous force is simple and easy to build and is useful in mechanical dissections, particularly where quick movements are not required. It can be used even to work with the hanging-drop method. However for some operations it is too slow. For example, if we want an opening in the lung wall around a vessel and we try to bite away small bone chips, the cutting movements are often too slow for a good job to be done. For this purpose, what seems to be indicated is a reduction of the lateral movements by a lever system instead of by slowness.

Several models of lever manipulators were constructed and the type shown in Fig. 6-12 proved to be the simplest and most reliable. In this

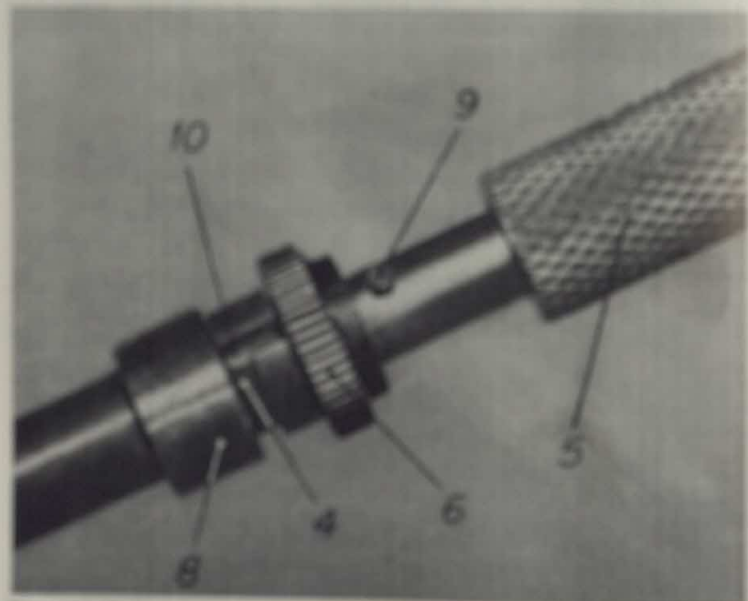


FIG. 6-12. Lever that permits an exchange of dissecting instruments with one hand.

model the displacement along the longitudinal axis of the handle is controlled by cinous forces in the same way as in Fig. 4-11. For the lateral movements tube 1 is attached to sphere 11 instead of a disk. The radius of this sphere is slightly larger than the distance between the tip of the instrument and the surface of the sphere. Therefore an upward displacement of handle 7 will produce a similar but greatly reduced displacement of the instrument. The sphere glides on a spherical ring attached by holder 12 to the tube of the microscope objective. To maintain a firm contact between the sphere and the ring, disk 13 is pressed against the ring by spring 14. Three steel balls decrease the friction between disk 13 and ring 12. Ring 13 slides on tube 1 while ring 14 is fixed.

This type of micromanipulator fulfills most of the requirements in as far as stability is concerned and makes some working under the microscope possible.

Experiments with this micromanipulator indicated that the stiffness of the finger tip holding the handle decreases with increasing stiffness of the handle system. If the handle shows no resistance to movement, the position of the hand is controlled only by the muscles of the arm.

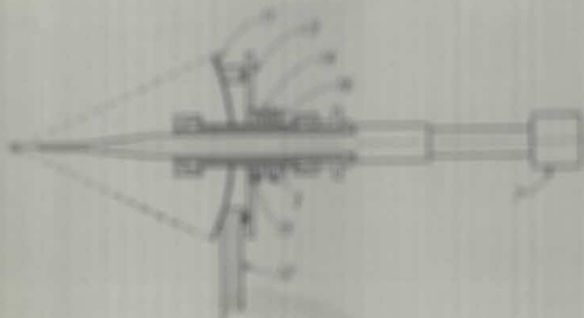


Fig. 4-15. Schematic micromanipulator with a ball tip of reflection for lateral movements and a spring reflection for longitudinal displacements of the handle.

and the involuntary displacements of the hand are very large. But if the handle has some stiffness, displacements of the hand produce almost no tip of the fingers which is very hard to steady the position of the hand.

For some special experiments, as on the blood circulation, maximal speed is necessary. Consequently all viscous forces must be avoided. For this purpose the lever system shown in Fig. 4-16 was developed to



Fig. 4-16. Construction of a handle that uses a lever system for the reflection of longitudinal movements.

It inside tube 1 of Fig. 4-15. The system consists of tube 12 in which wedge 18 slides. This wedge rotates lever 15 around its pivot 20 so that the short arm of the lever displaces the instrument tool at the tip of 21 in the longitudinal direction. Spring 22 is used for return motion and to avoid backlash. Figure 4-17 is a photograph of this micromanipulator.

The handles of the operative tool shown in Fig. 4-15 are made light enough in weight so that gravitational forces will not cause them to slide downward when they are released. However, because of its increased

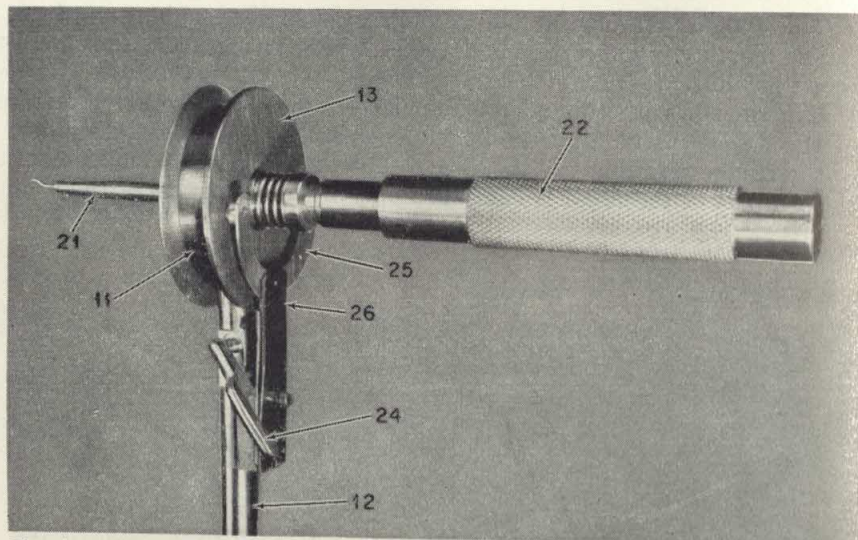


FIG. 4-15. Spherical micromanipulator with a lever type of longitudinal displacement.

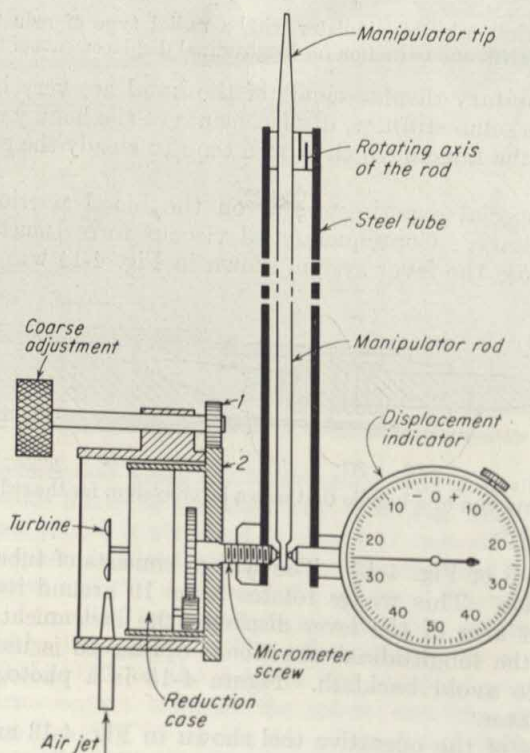


FIG. 4-16. The air-driven micromanipulator. A turbine attached to a reducing gear produces lateral displacements of the manipulator rod, which can be read on an indicator.

weight, the handle shown in Fig. 4-14 has a tendency to slide downward very slowly. To prevent this, the device shown in Fig. 4-15 has been provided to lock it in position. In the locked position, spring 26 presses fork 25 against disk 13. Raising handle 24 lifts the spring and releases the lock.

The coarse adjustment of the micromanipulator is obtained by permanently attaching handle 12 to the tube of the microscope objective in

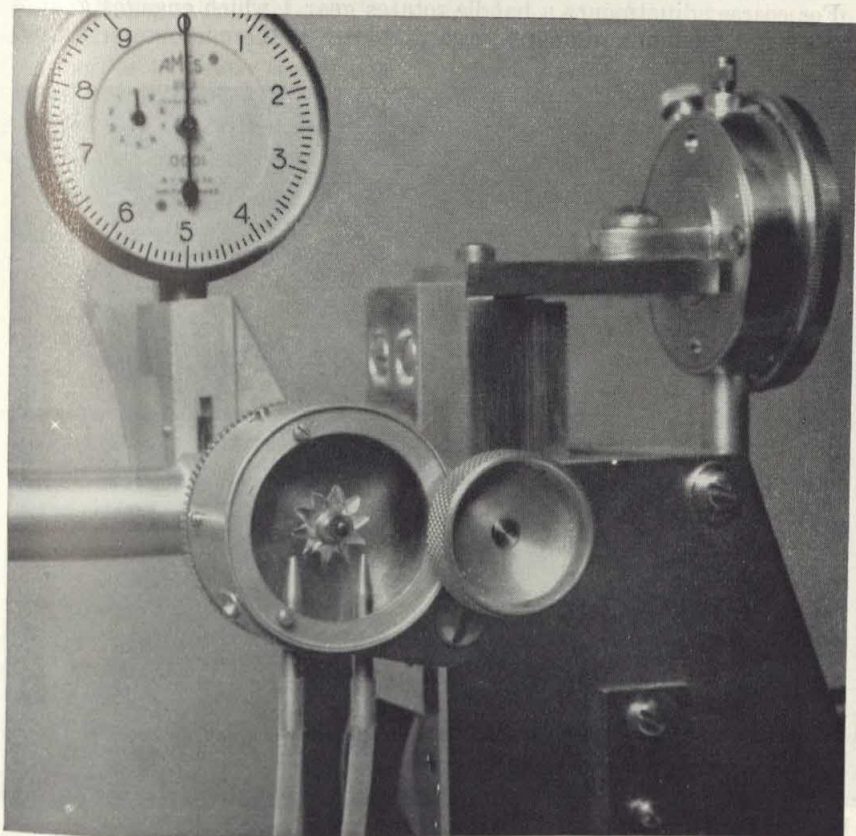


FIG. 4-17. Photograph of the manipulator. Note that two nozzles are provided, for forward and reverse motions.

such a way that the tip of the operating instrument moves in the middle of the focused field of view of the microscope.

Air-driven Micromanipulator. For extremely delicate movements a motor-driven manipulator is superior to a micromanipulator in which the hand is used to produce the displacements because motor-driven movements are much smoother. The micromanipulator to be described is controlled by two switches, each with three positions. The first switch moves the manipulator up or down or holds it without movement. The second switch controls movements to the right and left.

A small air-jet turbine is used as a motor. The wheel of the turbine

is made from an aluminum sheet 0.1 mm thick and is carefully centered dynamically so that the turbine does not produce vibrations. As shown in Fig. 4-16, the turbine is connected to a reduction case and a micrometer screw so that 25,000 rotations of the turbine produce a 1-mm displacement of the manipulator tip. The size of the displacements can be measured on a displacement indicator, and backlash is eliminated by using a spring as the rotating axis of the manipulator rod.

For coarse adjustments a handle rotates gear 1 which engages gear 2 and rotates the whole reduction case and with it the micrometer screw.

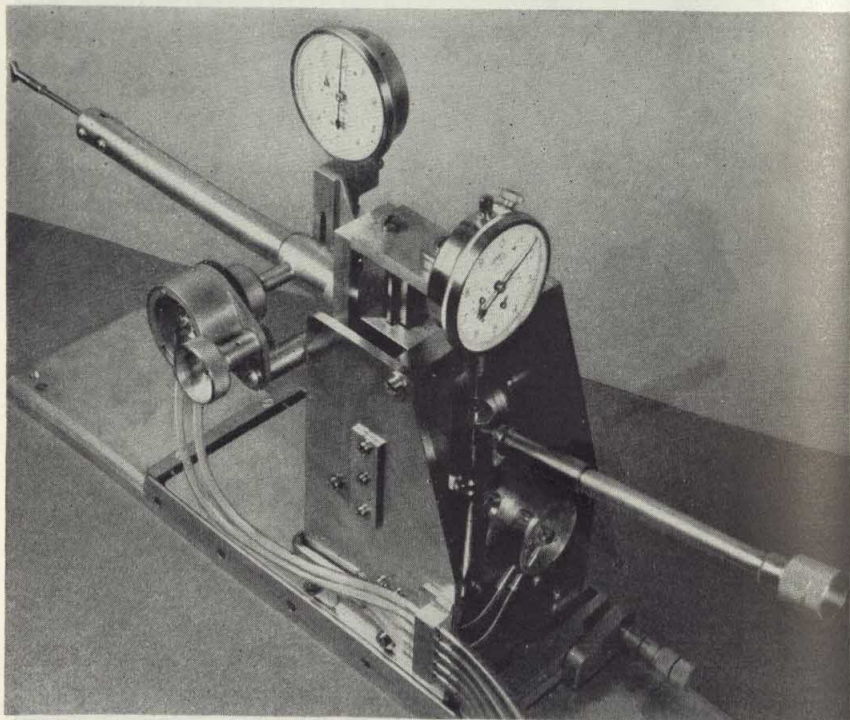


FIG. 4-18. Arrangement of two mechanisms to obtain vertical as well as horizontal displacements. The long arm and thumbscrew to the right is the coarse adjustment for vertical movements.

The micrometer screw is made to move with the case because the large gear reduction would make it necessary to exert a great force in order to rotate the screw relative to the case if the force were applied to the screw. But a small stream applied to the turbine is sufficient to rotate the screw relative to the case, as in this situation the speed is reduced and the forces are correspondingly increased.

When vertical displacements are needed also, a second mechanism is used to operate a rack-and-pinion movement that carries the first mechanism, as shown in Fig. 4-17. Figure 4-18 gives another view of this

arrangement. Note that two nozzles are provided to give forward and reverse motion.

The motor-driven apparatus has the following advantages: (1) The automatic drive leaves the hands free during movements of the manipulator. (2) As there is no need to touch the manipulator, vibrations are avoided. (3) The movements obtained can be read on a scale. (4) The manipulator can be controlled from another room. (5) It is possible to have all the movements of the manipulator completely automatic, in accordance with a predetermined program.

In order to render the manipulator automatic, the program of movements can be presented in the form of a perforated paper tape similar to that used in telegraphy. The tape is moved at a given speed along a set of feeler pins that activate a magnetic valve (shown in Fig. 4-19).

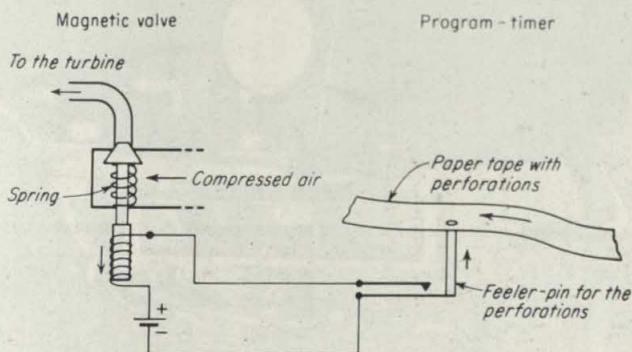


FIG. 4-19. Method of programming of manipulations.

Four such valves conduct compressed air to the four jets at predetermined time intervals, thereby carrying out a series of movements in two dimensions.

Both of these manipulators have been used in investigations of the organ of Corti.

EQUIPMENT FOR PRODUCING A KNOWN DISPLACEMENT AND PRESSURE ON THE COCHLEAR PARTITION*

For measuring the pressure applied by a needle to the cochlear partition a mechano-electronic transducer tube (RCA 5734) has been used. A long lever is soldered to the movable arm of the tube, as shown in Fig. 4-20, and a stimulating needle *n* is attached to this lever. A rotation of the lever in the plane of the figure changes the position of the grid of the tube relative to the anode and causes a change in the anode current. The lever *l* has two symmetrical arms *a* extending around the tube. The mass of these arms is adjusted so that the center of gravity of the needle and lever coincides with the point of rotation of the movable arm of the tube. Therefore vertical displacements of the tube and lever

* Extract from Art. 61 as listed in the Author's Bibliography. Published in 1951.

system do not produce any rotation and hence produce no change in the anode current in spite of the fact that the tube is sensitive to vertical pressures on the tip of the needle. This makes it possible to mount the whole system on a vibrating table, which can be set into vertical motion by the electromagnetic unit *E*. To ensure a movement free of rotation a flat, triangular spring *S* is used. The spring is fixed at its center to the holder *H* by means of a screw with a hole through it. A rod from the electromagnetic unit extends through this hole to transmit the vibration to the plate *P* on which the tube is mounted.

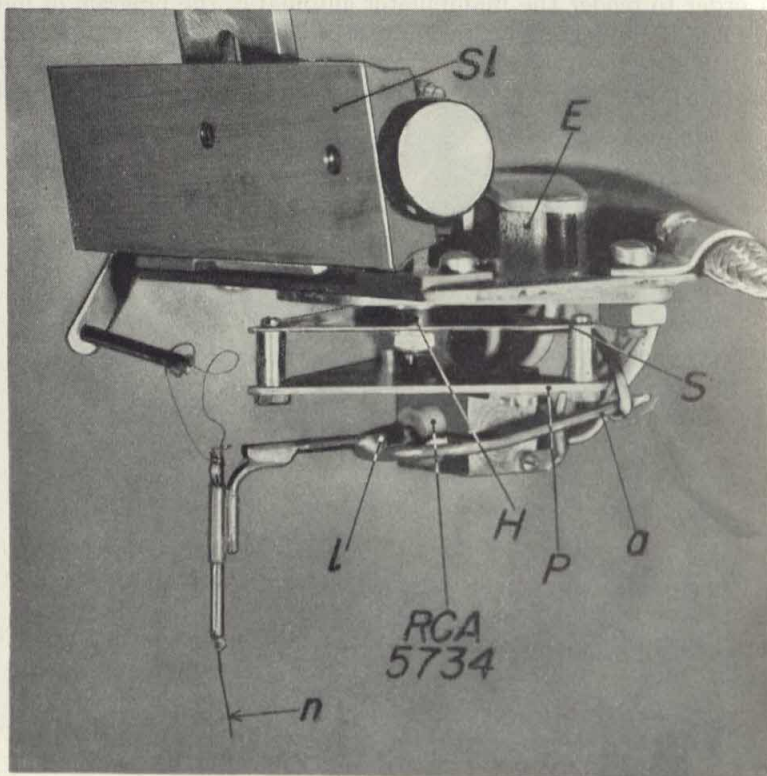


FIG. 4-20. Apparatus for producing a known displacement and pressure.

The electromagnetic unit was used to produce small displacements of the tube of known amplitude. It was established by special measurements that the stiffness of the point of the needle for vertical displacements was at least ten times that of the cochlear partition. Consequently, the vertical displacement of the needle point when pressing on the cochlear partition will be the same as that of the tube, with a tolerance of 10 per cent.

Because an extremely thin wire was used as the end portion of the needle *n*, a displacement of the tube in the horizontal plane produced microphonics that were no larger than 10 per cent of the vertical dis-

placement. A lateral pressure on the needle point was not registered by the tube.

The system was calibrated with a spring of known stiffness, so that the pressure at the tip of the needle could be read in dynes on an oscilloscope. A slide S_1 served to attach the whole equipment to a microscope.

This equipment indicates the pressure changes produced by given displacements and therefore gives measurements of mechanical impedance.

MEASUREMENT OF THE VIBRATORY AMPLITUDE OF A SOLID OBJECT*

Particular difficulties are encountered in measuring the vibratory amplitudes of a solid object, such as the body of a violin, the sounding

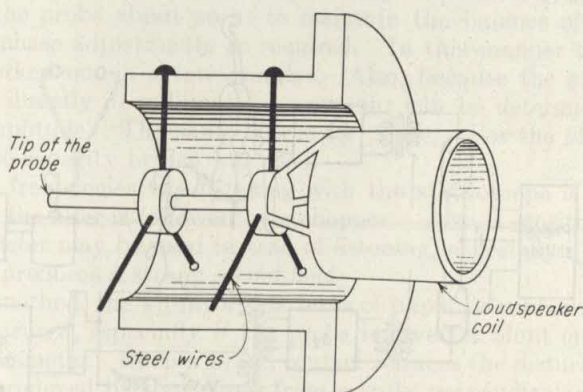


FIG. 4-21. The vibrating probe.

board of a piano, or a loudspeaker diaphragm, because loading the object with ordinary kinds of measuring apparatus produces a significant change in the nature of the vibration. A method was devised to overcome these difficulties.

If a vibrating probe is used to make contact with a vibrating object, then usually the vibration of both probe and object will be altered. This will not happen, however, if the vibrations of the probe are given exactly the same frequency, amplitude, and phase as the vibrating object. Then, provided that the elastic limits of object and probe are not exceeded, the two vibrations simply coexist and the application of the probe has no effect except to alter the position of static equilibrium of the two bodies.

Therefore, the vibratory amplitude can be measured at any point by adjusting the amplitude and phase of the probe until a contact with the object has no effect upon the vibrations of the probe.

The probe is shown in Fig. 4-21. It consists of a thin metal rod connected to an electrodynamic loudspeaker coil by means of six fine steel

* Extract from Art. 8 as listed in the Author's Bibliography. Published in 1931.

wires. The mounting is such that the rod can be displaced only along its longitudinal axis.

Any alteration of the manner of vibration of the probe produces a change in the impedance of the electrodynamic driving system, and this change is easily observed by means of an a-c bridge (see also Gerlach). The complete circuit is shown in Fig. 4-22. The bridge is formed by the two coils of the transformer through which the energizing current is applied, the electrodynamic coil, and a variable arm consisting of resistance R and inductance L . The detector consists of an amplifier followed by a filter and then by a loudspeaker unit working into a pair of stethoscope tubes.

The bridge is balanced, with the probe free of any contact, by adjusting R and L for a minimum of tone as heard in the stethoscope tubes.

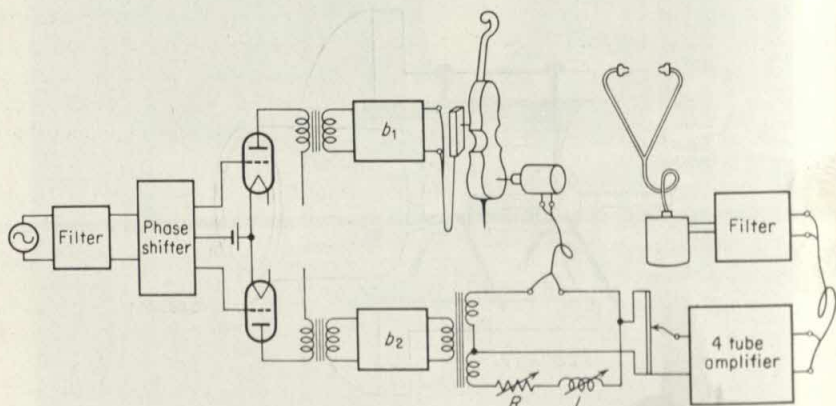


FIG. 4-22. Bridge circuit used with a probe for the measurement of amplitude and phase.

Then the least contact with the probe, as with a thread or hair, will easily be noted as a reappearance of the tone.

The vibratory amplitude of the probe is adjusted by means of attenuator b_2 . By a choice of high-grade steel wires for the suspension of the coil, it is possible to obtain a satisfactory degree of constancy of the impedance of this coil when it is not loaded. Its impedance can be kept within 0.5 per cent even when its amplitude of vibration is varied up to 0.05 mm. Accordingly, only minor adjustments of the bridge are necessary to keep it in balance after changes are made in the setting of attenuator b_2 . Likewise, the proportionality between the bridge current and the vibratory amplitude is maintained with the same precision.

Because of this constancy of operation, it is possible to calibrate the probe by adjusting it for large amplitudes and measuring these amplitudes with a microscope. Smaller amplitudes are then obtained by use of the attenuator.

The vibrating body that is to be investigated, such as the violincello illustrated in Fig. 4-22, is driven by the electrodynamic vibrator con-

trolled by attenuator b_1 . This vibrator may be applied to one of the strings or to the bridge of the instrument.

The stethoscope tubes in the ears are helpful in balancing the bridge, because they reduce the disturbing sounds radiated into the air by the instrument.

By means of the phase shifter and attenuator b_2 it is easy to show that the making of the contact with the vibrating body does not itself disturb the minimum of the bridge. There is only a noise at the moment of contact, which is likewise present when no alternating current is passed through the bridge. With a four-stage amplifier and proper shielding of the bridge (not shown in the figure), amplitudes as small as 10^{-4} mm can be measured within 1 or 2 per cent.

To determine contours of equal amplitudes over the surface of the vibrating object it is only necessary to keep attenuator b_2 constant and to move the probe about so as to maintain the balance of the bridge, and with phase adjustments as required. In this manner the contours can be worked out in a few minutes. Also, because the probe can be calibrated directly in millimeters, a contour can be determined for any desired amplitude. The same is true for phase. For the phase shifter, a resistance-capacity bridge was used.

For low frequencies the listening with the stethoscope is made more effective if the filter is followed by a chopper. Also, a sensitive vacuum-tube voltmeter may be used instead of listening, especially if the vibrating object produces a strong sound field.

By this method, the vibratory patterns of paper or rubber diaphragms can be measured, especially if the probe is given a blunt end of about 0.5 cm in diameter. Such a broad contact reduces the disturbances that would be produced by deviations from a truly perpendicular placement of the probe.

CAPACITATIVE PROBE FOR THE MEASUREMENT OF VIBRATORY AMPLITUDES*

The vibrating probe method just described has certain limitations. It cannot be used for measuring the vibrations of very small objects, or objects so delicate that they cannot even be touched without damaging them or modifying their action, such as the eardrum or the basilar membrane. For such situations Backhaus (1,2) developed a method in which a piece of metal foil is attached to the vibrating surface and a second fixed electrode is placed a short distance away. These two conducting surfaces then form the plates of a condenser, and when one plate is vibrating the variations in capacity give a measure of the vibratory amplitude.

The magnitude of the capacitive variations depends upon the mean distance between the two conducting surfaces, and therefore it is necessary to control this distance. This is done by measuring the mean capacity of the condenser. The capacity of the condenser and its variations

* Extract from Art. 38 as listed in the Author's Bibliography. Published in 1941.

can be measured by using this probe condenser as a part of a high-frequency oscillator. The mean frequency of the oscillator then gives the value of the capacity, and at the same time the frequency modulation gives a measure of the vibratory amplitude of one of the condenser plates. By using the method of the half-resonance curve developed by Rieger the frequency modulation can be transformed into an amplitude modulation. A simple rectifier can be used to transform the amplitude modulations into a low-frequency alternating current, which is a measure of the mechanical vibratory amplitude.

This method has the drawback that when the electrode surface is made small the amplitude of modulation is correspondingly reduced, and hence the sensitivity is impaired. Therefore a circuit was looked for that would make the amplitude of modulation independent of the size of the electrode surface.

Such a circuit is shown in Fig. 4-23. The probe capacitance C is measured in terms of the alternating voltage across the resistance R ,

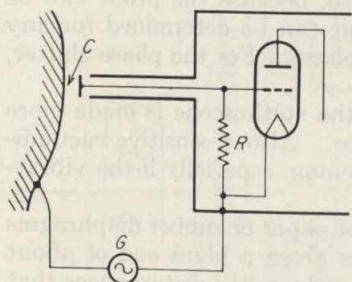


FIG. 4-23. The principle of the capacitive probe.

when from a source G a current of 100,000 cps is passed through R and the condenser C . When the impedance of C is much greater than that of R , the voltage across R is a measure of the impedance of C , provided that the generator voltage is kept constant. A change in the separation of the electrodes always produces the same percentage change of capacity and impedance, independently of the size of the electrode surface. Hence the amplitude of modulation is independent of electrode size. A reduction

in the size of the electrodes will make the carrier current smaller, but this can be compensated for by increasing R and increasing the subsequent amplification. Satisfactory measurements can be made with electrodes as small as 1 mm in diameter. It is only necessary that the probe electrode be carefully shielded, so that the currents through R shall be limited to those also passing through C .

The complete circuit is shown in Fig. 4-24. The first stage of the amplifier is double-shielded, and the 100,000-cps generator is connected between outer and inner shields. The capacity between these shields merely loads the generator and does not produce a current in resistance R . However, the stray field at the tip of the probe between outer and inner shields produces a small current in R . When the tip of the probe approaches an object, the stray voltage between the two shields is increased, producing a greater carrier current through C and R . This carrier current, modulated by the vibrations of the object, is transmitted inductively through slits cut in the two shields to the second amplifier stage and to a rectifier. The potentiometer P permits adjustment for the different values of carrier current arising from different sizes of electrode

surface. The rectifier is followed by a low-pass filter and a low-frequency amplifier, and finally by an a-c meter.

In making the measurements, the probe is made to approach the vibrating object until the plate current of the rectifier tube reaches a certain value, which represents a particular distance. Then, on the basis of a previous calibration, the vibratory amplitude can be determined from the reading of the a-c meter. The calibration is made by bringing the end of the probe close to a vibrator (see page 51) whose vibratory amplitude is great enough to be measured microscopically.

With an electrode of 1 mm diameter and a distance from the object of 0.5 mm it is possible to measure amplitudes as small as 10^{-6} cm. The sensitivity is limited by tube noise and also by irregularities in the output of the high-frequency generator, which after rectification appear as

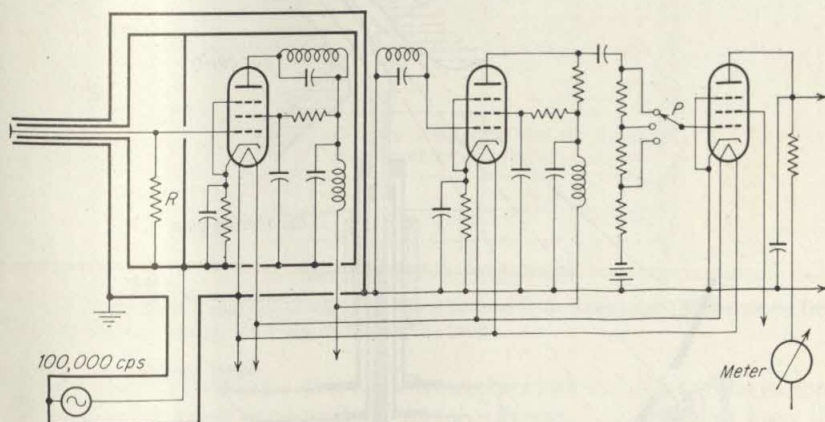


FIG. 4-24. Electrical circuit of the capacitive probe.

noise. Apparently also any alternating current flowing through a resistance is modulated to some degree (see Bernamont, Brillouin).

The probe is shown in greater detail in Fig. 4-25. A copper wire, flattened somewhat at the end, serves as the probe tip. Over this wire is pushed a thin catheter tube, and this tube is covered with aluminum foil held in place by winding with fine silk thread and painting with bakelite varnish. A second foil and varnish layer enclose the first. As the figure shows, these foils end at different places at the proximal end of the probe so as to connect each with its proper shield. Because most physiological measurements are made in deep cavities, the probe is bent at the end so that its position can be observed from one side with a head mirror.

The mechanical damping afforded by the layers of varnish prevents resonant vibrations of the probe. It is possible to glue the probe to the preparation so that undesirable movements between the two are avoided. In physiological studies in which the surfaces to be studied are usually

moist, it is well to coat the end of the probe with a water-repellent varnish, so that contact with the wet surface has no bad effects.

In experiments the probe proved satisfactory for practical use, for its sensitivity changed only 10 per cent when its angle of application to the surface varied as much as 30° from the vertical, provided that the tip was no closer to the surface than its own radius (about 1 mm). Therefore it is not necessary to use special care in its placement, but only to maintain the carrier current at a constant value.

Often over a surface there are abrupt changes in vibratory amplitude, as shown for example at the nodes of vibration of a membrane. Therefore it is important to determine to what extent the readings are affected

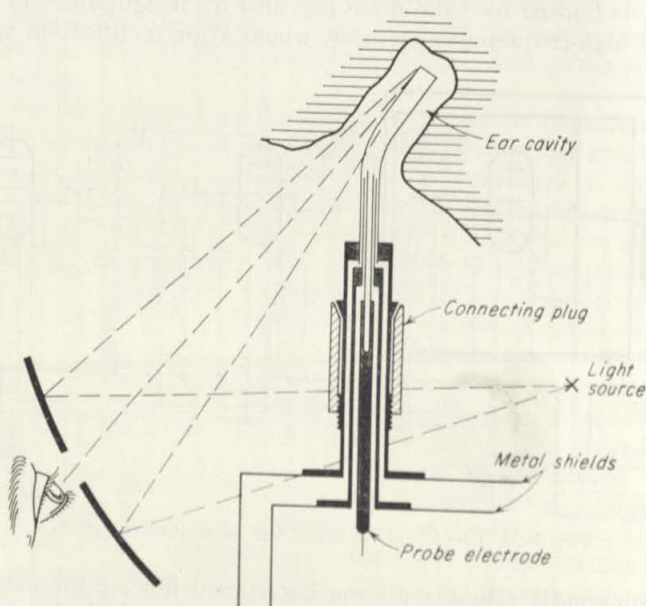


FIG. 4-25. Details of the probe tip.

by the vibrations of areas surrounding the probe and not immediately in front of it.

For this determination, the probe was mounted vertically above a smooth, flat metal plate, and a series of metal disks of uniform thickness but varying diameter were placed on the plate and concentric with the probe. Readings were made of the variations in the carrier current as a function of disk size, when this size varied from the diameter of the probe tip to 3.5 times this diameter. Figure 4-26 shows that when the distance of the probe from the vibrating surface is one-half the diameter of the tip the effect is practically restricted to that immediately under the tip. An increase of the vibrating area by 50 per cent over this amount produces only a 9 per cent rise in the reading, and a further increase produces only a 13 per cent rise. When the distance between the probe and the vibrating surface is greater, there is a significant

enlargement of the effective area. Therefore for practical measurements the distance is adjusted to half the diameter of the probe tip.

Measurements by this method do not always require that a metal foil be attached to the vibrating body. The stray capacity between the probe tip and the grounded outer shield is altered by a close approach to any material whose dielectric constant is greater than that of air. Thus it is possible without any special provisions to measure the vibratory amplitude of insulating materials. To investigate this variation of the method, a number of thick plates of various insulating substances

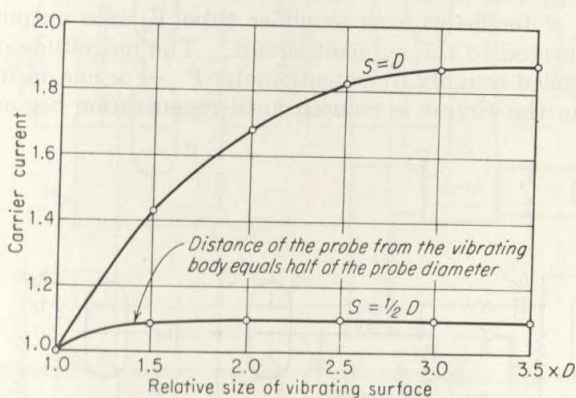


FIG. 4-26. Effect of the size of the vibrating surface. S = distance of the probe from the vibrating surface; D = diameter of the probe.

were glued to a vibrator and the effects observed with the probe in comparison with those produced by metal surfaces. In order to keep the carrier current constant it becomes necessary to bring the probe closer to the surface than is done for metals. The resulting increases in sensitivity are given for a few substances in Table 4-1.

TABLE 4-1

Material	Dielectric constant	Increase in sensitivity, per cent
Metal.....		0
Wood.....	6.8	15
Bakelite.....	5.4	20
Trolitul.....	2.2	30

For materials with large dielectric constants the differences are negligible. The vibratory amplitudes of thin membranes made of insulating materials can be measured, though account must be taken of the thickness of the membrane. The amplitude of vibration of loudspeaker diaphragms can easily be found.

APPARATUS FOR PRODUCING TONES WITH SLOW RATES OF ONSET AND DECAY*

Three systems have been used to produce various rates of onset and decay for continuous tones. One of these is presented in Fig. 4-27. A resonant circuit formed by inductance L , capacitance C , and resistances R_1 and R_2 was used to produce onset and decay times that could be varied by adjusting resistance R_2 .

To produce long times of onset and decay it is necessary to reduce the inherent energy loss of the resonant circuit. This can be done by the introduction of feedback from amplifier tube V_2 into output tube V_1 , which is connected to the resonant circuit. The magnitude of the feedback is controlled roughly by potentiometer P . For fine adjustment the energy loss in the circuit is reduced until regeneration begins and then

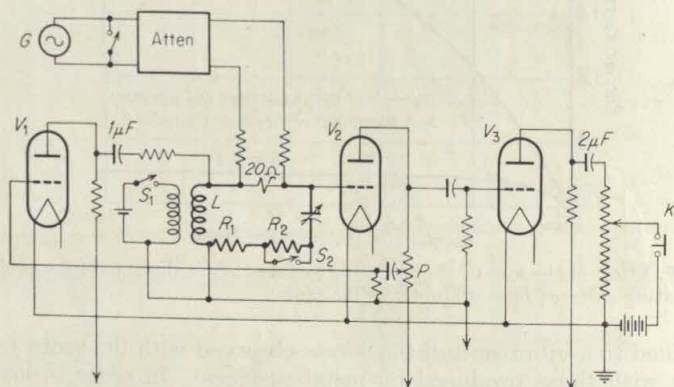


FIG. 4-27. Circuit for producing slow onset and decay of tones.

is increased until the regeneration just ceases. During these adjustments R_2 is kept at zero. Now if R_2 is raised in resistance it is possible to go from a practically undamped circuit to any desired degree of damping.

If under these conditions a sinusoidal current is suddenly applied from generator G it will appear at the output of V_3 with increasing amplitude, and then when switched off will die away.

The resonant circuit can also be excited by a sudden shock, such as is produced by opening switch S_1 to cause a rapid decrease in the magnetization of L through its secondary winding.

For very long times of onset and decay the circuit shown in Fig. 4-28 may be used. Here a condenser C is charged or discharged through a high resistance R by the battery V_0 . The condenser voltage is applied to the grids of the tubes V_1 and V_2 to control their amplification. By this means the amplitude can be changed by a ratio of about 1:50. The push-pull amplifiers are carefully balanced, so that a sudden change in

* Extract from Art. 14 as listed in the Author's Bibliography. Published in 1933.

the d-c potential of the grids does not produce a click in the transmitted tone.

When only one tone of constant frequency is needed, the equipment shown in Fig. 4-29 is used. Here the d-c voltage across a capacitor C

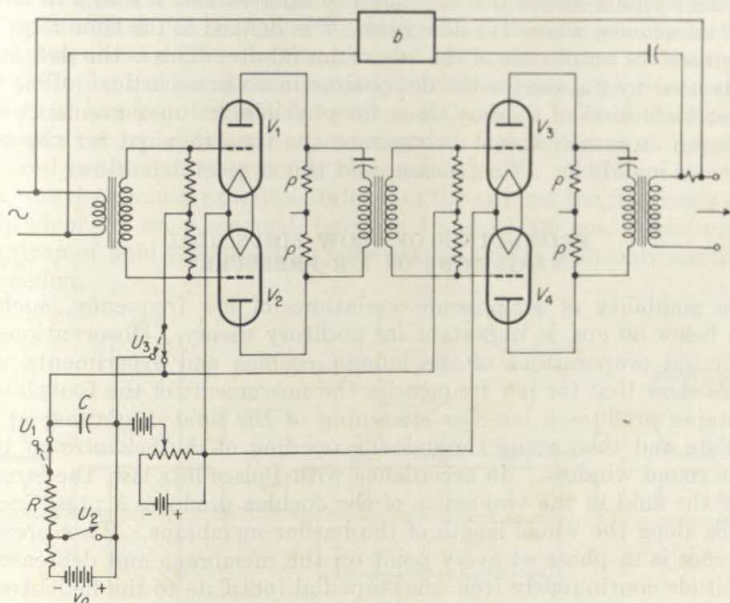


FIG. 4-28. Another circuit for producing slow onset and decay of tones.

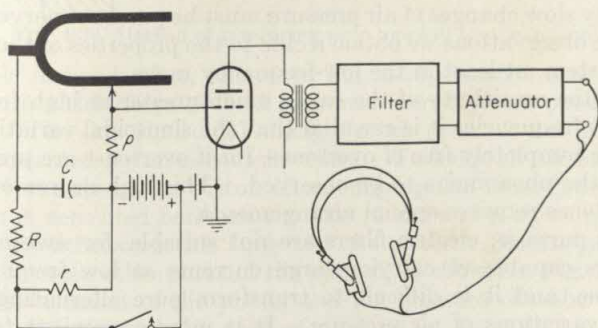


FIG. 4-29. A third circuit for producing a tone with slow onset and decay.

is interrupted periodically with a tuning-fork vibrator, amplified, and then filtered. The condenser is charged and discharged by use of the battery and a high series resistance R . The decay time of the condenser voltage is given by

$$T = 6.9CR \left(1 - \frac{R}{2\rho} \right)$$

where ρ is a high resistance in series with the tuning-fork interrupter. To have precise decay time, a mica condenser must be used to prevent aftereffects. The whole system was calibrated with automatic reverberation-measuring equipment.

In the formula above C is measured in microfarads, R and ρ in ohms, and T in seconds, where the decay time T is defined as the time required to decrease the amplitude of the vibrations 60 db. This is the definition as it is used by Sabine for the decay time in room acoustics. This is a physical definition of a decay time; for physiological measurements it is sometimes more convenient to measure the time required for the tone to become inaudible. Waetzmann used this type of definition.

PRODUCTION OF SLOW SINUSOIDAL VARIATIONS OF AIR PRESSURE*

The audibility of air-pressure variations of low frequency, such as those below 30 cps, is important for auditory theory. Observations on anatomical preparations of the human cochlea and experiments with models show that for low frequencies the movements of the footplate of the stapes produce a lamellar streaming of the fluid, beginning at the footplate and then going through the opening of the helicotrema back to the round window. In accordance with Poiseuille's law, the streaming of the fluid in the two scalae of the cochlea produces a pressure difference along the whole length of the basilar membrane. This pressure difference is in phase at every point on the membrane and decreases in magnitude continuously from the stapedial footplate to the helicotrema. It must be assumed that for these low frequencies a mechanical frequency analysis in the cochlea does not occur, and that the auditory phenomena produced by slow changes of air pressure must be purely of nervous origin. From these observations we obtain a clue to the properties of the auditory nervous system, at least in the low-frequency range.

Because the sensitivity of the ear is much greater at high frequencies than at low frequencies it is essential that the sinusoidal variations of air pressure be completely free of overtones, for if overtones are present they will mask the phenomena to be observed. This high degree of freedom from overtones requires special arrangements.

For this purpose, electric filters are not suitable, for several reasons. Such filters capable of carrying large currents at low frequencies are cumbersome, and it is difficult to transform pure alternating currents into pure variations of air pressure. It is more convenient to produce large sinusoidal air-pressure changes mechanically and to filter them mechanically.

Acoustic filters constructed as analogs of electric filters have the disadvantage that for very low frequencies their dimensions are impractically large (Wagner, 1; Stewart and Lindsay; Waetzmann and Noether). More convenient for this purpose are the semimechanical filters. But good results can be obtained only if care is taken that the vibrating

* Extract from Art. 22 as listed in the Author's Bibliography. Published in 1936.

masses have but one degree of freedom, so that the forces acting on the input to the filter can reach the output only in the assumed and calculated way. This requirement is sometimes hard to fulfill because of the appearance of disturbing vibrations, especially of high frequencies which travel as sound waves through the solid bodies and thereby pass around the entire filter. A second disturbing effect arises from the fact that there may be a change in the form of vibration of one of the masses. For example, if a membrane is made to vibrate above its resonance frequency it begins to vibrate in sections with nodes. Then the filter calculations become difficult, particularly when a high degree of damping is required in the frequency range concerned.

It was determined experimentally that throughout the frequency range with which we are concerned, between 1 and 10,000 cps, a fluid column or a drop of fluid vibrating in a tube acts as a mass with only one degree of freedom.

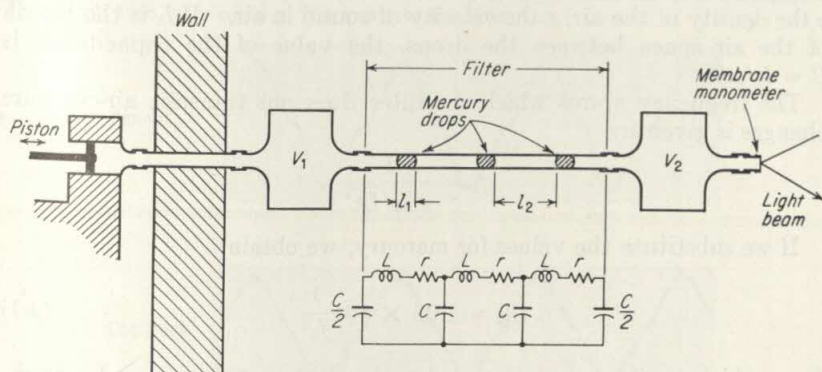


FIG. 4-30. Method of producing pure tones of low frequency.

A simple low-pass filter, shown in Fig. 4-30, consists of a horizontal glass tube in which drops of fluid (water or mercury) are placed at equal intervals. The slow sinusoidal changes of air pressure are produced by a piston operated by an eccentric wheel. To keep all air-borne sound and the vibrations of the piston from entering the observation room, a large tube is cemented between the two rooms and a short rubber connection is used between this tube and the piston. Similar connections are made between other parts of the system, as shown in Fig. 4-30. The volume displacement of the piston and the pressure chamber V_1 are so large that vibrations of the drop of fluid in the tube do not have any effect on the pressure in V_1 . Therefore the pressure variations at the entrance of the filter are independent of frequency. At the termination of the filter is another pressure chamber V_2 connected to a membrane manometer with a mirror, and also a tube that can be connected to the ear. It is desirable that V_2 be made large enough that vibrations of the drops of fluid caused by building vibrations do not produce audible pressure changes in the ear. Furthermore, it is important that the rubber tubes connecting the pressure chambers and the filter are not so long as

to undergo appreciable elongation and compression in response to the air-pressure changes, for such action will set up longitudinal vibrations of the whole system.

A diagram of the mechanical filter and also its electrical analog (see Hähne; Firestone, 1) are shown in Fig. 4-30. The capillary forces on the drops of fluid are neglected in the analog. If ρ_1 is the density, l_1 the length of one drop, and S the cross-sectional area of the tube, the mass of the drop corresponds to the inductance L , and $L = \rho_1 l_1 S$. Capacitance in the filter is produced by the elasticity of the air space between two drops, and is given by

$$C = \frac{\text{displacement}}{\text{force}}$$

A volume change dV of a closed air space produces a pressure $P = \rho c^2 dV/V$, where V is the volume of the space between the drops, ρ the density of the air, c the velocity of sound in air. If l_2 is the length of the air space between the drops, the value of the capacitance is $C = l_2 / \rho c^2 S$.

The frequency above which the filter does not transmit air-pressure changes is given by

$$f_0 = \frac{1}{\pi \sqrt{LC}}$$

If we substitute the values for mercury, we obtain

$$l_1 l_2 = 1.06 \times 10^4 \frac{1}{f_0^2} \quad (4-1)$$

from which a simple calculation for the filter network may be made. The length of the mercury drop l_1 should be as small as possible in order to minimize frictional force, for as may be seen in the electrical analog, any increase in the resistance r decreases the sharpness of the filter action.

A mercury-drop filter consisting of five sections was constructed with $l_1 = 2.3$ cm, $l_2 = 8.5$ cm, and an inside diameter for the tube of 0.25 cm. It was tested by registering photographically the movements of the manometer membrane while varying the motor speed continuously over a wide range. Results for three frequencies are shown in Fig. 4-31. The cutoff frequency as computed from Eq. (4-1) was 23.3 cps. It is seen that a fundamental of 13.3 cps is transmitted without loss, while its first overtone of 26.6 cps is reduced by 37 db. This action corresponds approximately to that of a three-section electric filter with proper impedance matching between input and output, but there is no such matching here.

In fluid filters also the operation can be improved by proper matching of impedances. Here it would be necessary to connect the filter to mechanical resistances instead of the pressure chambers V_1 and V_2 . A mechanical resistance can be calculated from the analogous electrical impedance. However, it is best that this procedure be omitted for two reasons: (1) it is convenient to control the pressure amplitude by vary-

ing the size of the chamber, and (2) distortions arise from the funnel action at the ends of the capillaries.

To study this funnel action, V_2 was reduced to 10 cu cm, the pressure changes were given an effective value of 10^3 dynes per sq cm, and V_2 was connected to the outer room by three different kinds of openings: (1) through a small funnel with an opening 0.5 mm in diameter, (2) through a capillary 1.5 cm long and 0.6 mm in inside diameter, and (3)

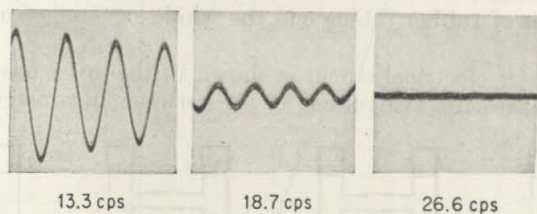


FIG. 4-31. Action of a five-section mercury-drop filter on three different frequencies. The amplitudes were equal at the input to the filter.

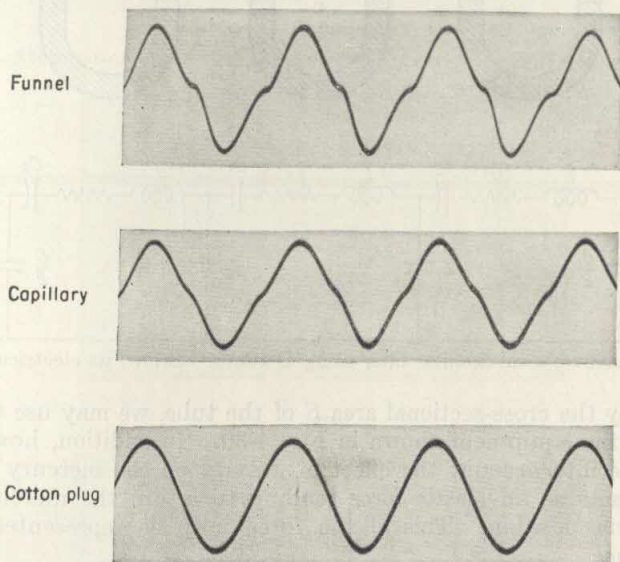


FIG. 4-32. Effects of three types of openings in the volume chamber on the end of the filter.

through a plug of cotton with the same streaming resistance as the capillary. Figure 4-32 compares the waveforms for the pressure in V_2 obtained by these three arrangements and shows that the cotton plug gives the best results. Distortion arises in the funnel because the quantity of air passing through it is not proportional to the pressure, so that there is always too much or too little air in the pressure chamber. The distortion is reduced if the chamber is made so large as to minimize this error. The distortion produced by the capillary can be reduced also by making it so long that the disturbing forces at its ends are small relative to the normal Poiseuille frictions.

A disadvantage of the straight horizontal filter is that the inside diameter of the tube cannot be larger than 3 mm, because for larger diameters the surface tension of the mercury is insufficient to keep the drop together when the vibratory amplitude exceeds 1 cm. Therefore for large volume displacements the apparatus shown in Fig. 4-33 was used, in which the filter consists of a series of U tubes. To prevent the transmission of vibrations from one U tube to another they are interconnected by short pieces of rubber tubing and the whole system is fixed to a large mass.

The analogous electrical circuit is shown in the lower drawing of Fig. 4-33. If l_2 represents the volume of air between two mercury columns

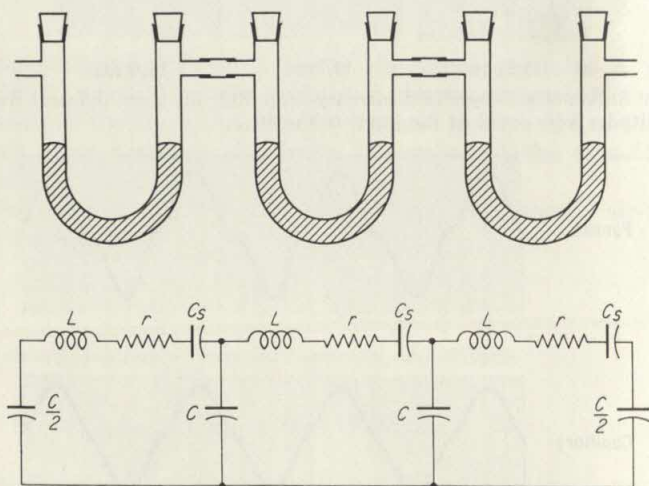


FIG. 4-33. Above, a mechanical filter using U tubes. Below, its electrical analogy.

divided by the cross-sectional area S of the tube, we may use the equations for the equipment shown in Fig. 4-30. In addition, however, we must take into account the effect of gravity on the mercury columns. Gravity acts as an elastic force tending to return the mercury to its equilibrium position. This elastic force may be represented by the capacitance

$$C_s = \frac{\text{displacement}}{\text{force}} = \frac{1}{2S\rho_1 g}$$

where g is the gravitational constant.

Such a filter acts as a bandpass filter that transmits frequencies between f_1 and f_2 . The cutoff frequencies are given by the equations

$$f_1 = \frac{1}{2\pi(LC_s)^{1/2}} = \frac{1}{\pi} \left(\frac{g}{2l_1} \right)^{1/2}$$

$$f_2 = \frac{1}{2\pi} \left(\frac{1}{LC_s} + \frac{4}{LC} \right)^{1/2} = \frac{1}{\pi} \left(\frac{g}{2l_1} + \frac{\rho}{\rho_1} \times \frac{c^2}{l_1 l_2} \right)^{1/2}$$

In a filter used for a frequency of 7 cps, the inside diameter of the tube was 1.8 cm, the length of the mercury column was 20.2 cm, and the length of the air column was 9.6 cm. The cutoff frequencies were 1.6 cps and 7.5 cps. Figure 4-34 shows the filter action for pressure

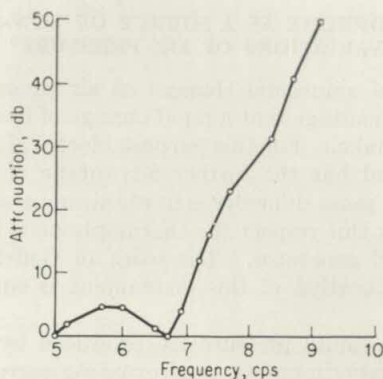
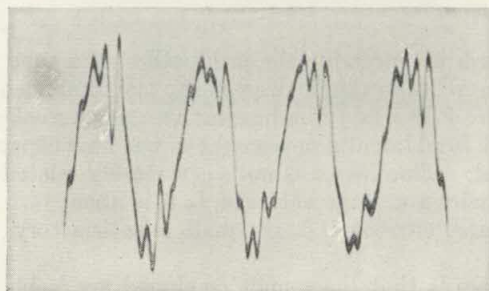
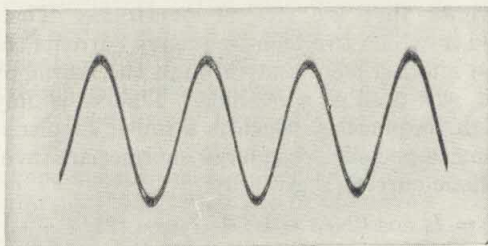


FIG. 4-34. Attenuation curve for a three-section filter with a cutoff frequency of 7 cps.



Input



Output

FIG. 4-35. Effects of the 7-cps filter on waveform.

chambers whose volume was 250 cu cm. Because a larger tube is used and the friction of the fluid column is smaller than in the setup of Fig. 4-30, the filter action is correspondingly greater.

To bring out clearly the action of this filter, the pressure variations

produced by the pump were made as distorted as possible, as shown in the upper curve of Fig. 4-35. The effectiveness of the filter is shown in the lower curve of this figure.

THE THERMOPHONE AS A SOURCE OF LOW-FREQUENCY VARIATIONS OF AIR PRESSURE*

The production of sinusoidal changes of air pressure by mechanical means has the disadvantage that a rapid change of frequency or of amplitude is difficult to make. For this purpose electrical equipment is much more convenient and has the further advantage of freedom from disturbing noise. The main difficulty is in obtaining a satisfactory freedom from overtones. In this respect the thermophone is far better than any other form of sound generator. The work of Geffcken and Keibs has shown that the calibration of this instrument is simple and that it is highly stable.

When changes of sound pressure are produced by a thermophone in the usual way, by superimposing an alternating current $I_1 \cos 2\pi ft$ upon a direct current I_0 , the energy consumption is represented by the equation

$$(I_0 + I_1 \cos 2\pi ft)^2 = I_0^2 + \frac{1}{2}I_1^2 + 2I_0I_1 \cos 2\pi ft + \frac{1}{2}I_1^2 \cos (2\pi \times 2ft)$$

where the last term represents the production of a tone of double frequency $2f$. The relation of this overtone to the fundamental is given by $(\frac{1}{4}I_1/I_0)F$, where F is a factor indicating how much weaker the overtone is relative to the fundamental on account of the heat capacity of the conductive material. This factor is not very closely related to frequency. For Wollaston wire and large values of I_0 it is about $\frac{1}{3}$. Hence as long as the alternating current is kept small a satisfactory purity can be achieved.

A disadvantage is that the sounds produced are feeble even for large currents, and the currents cannot be increased greatly because the conducting wire will burn out. Besides, it is difficult to produce very slow alternating currents that are free of overtones. Therefore another method was tried in which two high-frequency currents that were slowly beating with one another were sent through the thermophone, and this instrument itself was used as a rectifier. Then it is only necessary to filter out the high frequencies, which is a much simpler task than low-frequency filtering, especially when large energies are involved.

The thermophone current is given by

$$I = I_1 \cos (2\pi f_1 t - \epsilon_1) + I_2 \cos (2\pi f_2 t - \epsilon_2)$$

where I_1 , I_2 , f_1 , f_2 , ϵ_1 , and ϵ_2 represent the closely similar amplitudes, frequencies, and phases of the two alternating currents. Then I can be represented as $I = R \cos (2\pi f_1 t - \theta)$, where

$$R^2 = I_1^2 + I_2^2 + 2I_1I_2 \cos [2\pi(f_1 - f_2)t + \epsilon_2 - \epsilon_1]$$

and θ represents the slowly varying phase angle. From this equation

* Extract from Art. 22 as listed in the Author's Bibliography. Published in 1936.

we obtain

$$I^2 = \frac{1}{2}(I_1^2 + I_2^2) + I_1 I_2 \cos [2\pi(f_1 - f_2)t + \epsilon_2 - \epsilon_1] + \frac{1}{2}R^2 \cos (2\pi 2f_1 t - 2\theta) \quad (4-2)$$

If the frequency of the two beating currents is made sufficiently high, then only the slow variations with a frequency of $f_1 - f_2$ are audible, irrespective of the relation between the two current amplitudes I_1 and I_2 . These currents also can be made equal, giving a maximum of sound production.

The circuit arrangement is shown in Fig. 4-36. The two oscillators G_1 and G_2 , whose frequencies are preferably around 7000 cps, are filtered and attenuated and then superimposed in a bridge. When the bridge is properly balanced by means of resistance R , there is no interaction

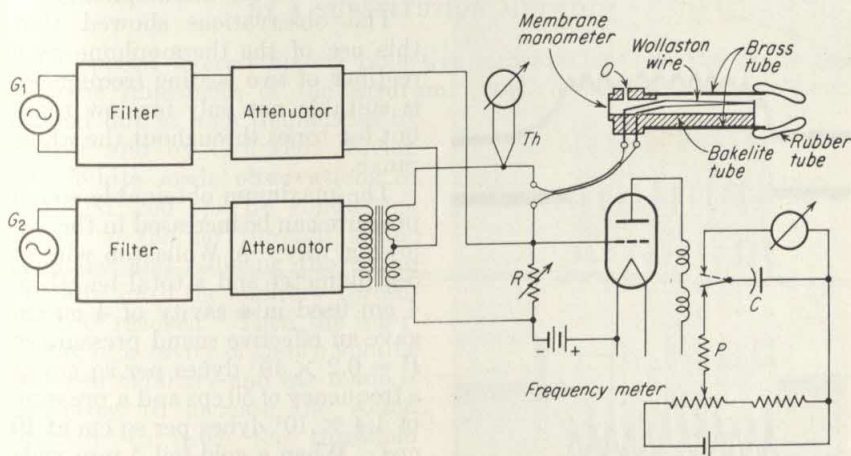


FIG. 4-36. Thermophone circuit for producing pure low tones.

between the two oscillators. The beat frequency across R is rectified by a vacuum tube and operates a relay that discharges a condenser C at the rate of the beats. The resulting current is read on a milliammeter and after calibration gives an indication of the beat frequency. The potentiometer P is used to set the meter to a standard frequency of 50 cps.

The thermophone consists of a bakelite tube closed at one end by a manometer membrane. The other end of the tube is reduced to half its diameter and contains the thermophone wires. This tube makes an airtight fit to a brass tube of 7-mm diameter that is provided with a rubber ring to make an airtight seal in the auditory meatus. The small opening O is provided with a cover that can be sealed in place with petroleum jelly after insertion of the earpiece into the meatus. This is to prevent alterations of air pressure in the meatus during insertion of the earpiece. The membrane manometer can be calibrated with static pressure, and its natural frequency and damping are determined by pull-

ing on it. All the measurements are made at frequencies below this natural frequency. If in Eq. (4-2) I_1^2 and I_2^2 are kept constant, the average temperature of the thermophone remains the same and its sensitivity is constant. Then the sound pressure is proportional to $I_1 I_2$, as was verified with sufficient accuracy by direct measurement. It is there-

fore possible to calibrate the thermophone for large currents at various frequencies by means of the membrane manometer, and then to calculate smaller sound pressures from the product $I_1 I_2$. Also the value of $I_1 I_2$ may be obtained directly by inserting a thermoelement in series with the thermophone.

The observations showed that this use of the thermophone as a rectifier of two beating frequencies is suitable not only for low tones but for tones throughout the whole range.

The maximum obtainable sound pressure can be increased in the following way. A Wollaston wire of $5\text{-}\mu$ diameter and a total length of 4 cm used in a cavity of 4 cu cm gave an effective sound pressure of $P = 0.2 \times 10^3$ dynes per sq cm at a frequency of 50 cps and a pressure of 1.4×10^3 dynes per sq cm at 10 cps. When a gold foil 5 mm wide and 4 cm long was used in the same cavity the pressure was 3×10^3 dynes per sq cm at 50 cps and 20×10^3 dynes per sq cm at 10 cps, even though the weight of the thermophone was less than 1 gram. Tones above 2000 cps were strong enough to be audible in the room several meters away. Accordingly, it is possible with a thermophone to make threshold measurements in a free sound field with little disturbance from overtones. However, there is an undesirable heat output

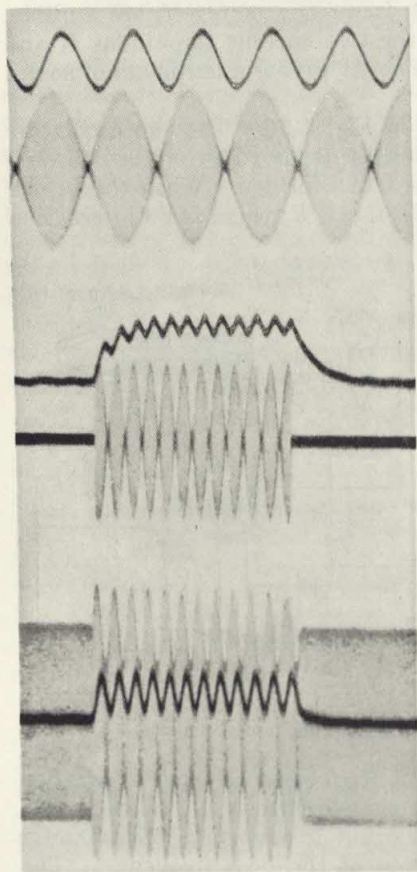


FIG. 4-37. All three portions show a phase shift between the combined high-frequency currents and their beat frequency. The middle portion shows also that there is a slow onset of the beat frequency when there is no preheating of the thermophone. The lower portion shows a rapid onset when the thermophone is preheated.

from the thermophone, so that ordinarily it is switched on only for brief periods. The warming of the air in the meatus is often unpleasant. This can be avoided by placing a thin rubber membrane between the ear and the thermophone wire, but such a measure is seldom necessary.

To ascertain the extent to which the thermophone is useful as a sound source for determinations of acoustic impedance, measurements were made simultaneously of both the varying current and the resulting sound pressure. At low frequencies there is a phase difference of nearly 90° between these two. This phase shift has a complicated relation to the beat frequency. The shift is shown in the upper portion of Fig. 4-37. Also the lower portions of this figure show that the thermophone is suitable for the production of brief tone pulses at low frequencies only if the thermophone is preheated with a steady current that is at least four times as large as the pulse. Otherwise the direct pressure changes are undesirably great. At higher frequencies this condition is even worse.

MEASUREMENTS OF THE ACOUSTIC IMPEDANCE OF THE EARDRUM BY A SUBSTITUTION METHOD*

Of special interest among objective measurements of the ear is the acoustic impedance of the eardrum. Such measurements have been carried out at high frequencies by Tröger and by Geffcken. Sivian and White made observations at 100 and 200 cps by conducting sound to the ear through a fine capillary and reducing the sound pressure until the auditory threshold was reached. Then the interposing of a cavity of known volume between capillary and ear made it necessary to increase the sound pressure to reach the threshold once more. The values of these two sound pressures made it possible to determine what volume would have the same compliance as the eardrum. This method has the advantage of giving impedance measurements for sounds at the auditory threshold.

For frequencies below 30 cps the threshold pressure is so great that simple impedance measurements can be made even below threshold. For this purpose a small T tube with an inside diameter of 7 mm is used, in the stem of which a long, narrow capillary is inserted, as Fig. 4-38 shows. The right arm of the T tube is closed by a small manometer membrane M_2 , on which is a mirror that deflects a light beam. For high

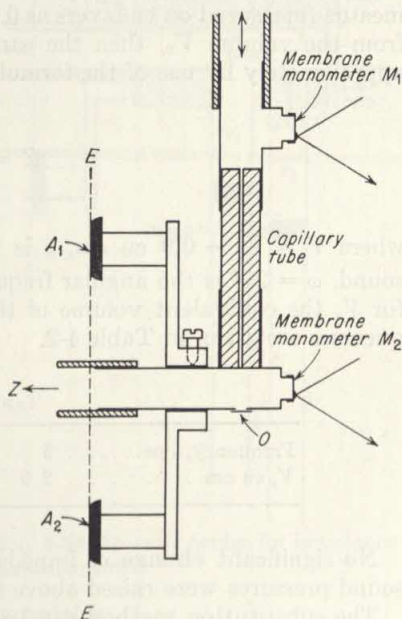


FIG. 4-38. Apparatus for measuring acoustic impedance by a substitution method.

* Extract from Art. 22 as listed in the Author's Bibliography. Published in 1936.

sensitivity this membrane is small and is made of a self-vulcanizing rubber solution. The left arm of the T tube is connected to the auditory meatus by a piece of rubber tubing and made airtight with petroleum jelly. A small hole O is provided to prevent damage to the membrane by an increase of air pressure when the earpiece is inserted into the meatus. After this insertion the hole is closed with a plate smeared with petroleum jelly. Two headrests A_1 and A_2 are then brought in contact with the head to fix the lateral portion of the cheekbone and the posterior portion of the temporal bone. Thereby the head can always be brought back to the same position. Also the stops determine the plane $E - E$, which represents the end of the meatus inside the auricle.

Since at low frequencies the eardrum is essentially a stretched membrane, its impedance is equivalent to that of an air cavity. Therefore the measurements may be carried out by applying pressure variations to the capillary and observing the resulting deflections of the manometer membrane. Then the ear is replaced with a variable cavity, such as an injection syringe, and its volume is changed until the same deflections are observed for the same pressure variations. If the volume of the meatus (measured on cadavers as 0.9 cu cm on the average) is subtracted from the volume V_0 , then the eardrum impedance can be determined approximately by use of the formula (see page 136)

$$Z = \frac{\rho c^2}{i\omega V} \quad (4-3)$$

where $V = V_0 - 0.9$ cu cm, ρ is the density of air, c the velocity of sound, $\omega = 2\pi f$ is the angular frequency, and $i = \sqrt{-1}$. Mean values for V , the equivalent volume of the eardrum, obtained at various frequencies are given in Table 4-2.

TABLE 4-2

Frequency, cps.....	5	10	20	30
V , cu cm.....	2.0	1.9	1.5	1.2

No significant change of impedance was observed when the applied sound pressures were raised above the auditory threshold.

The substitution method can be used also to determine the phase of the ear's impedance. For this purpose the bore of the capillary is made so small that the flow of air follows Poiseuille's law at the frequencies concerned. Then, as Fig. 4-38 shows, another membrane with mirror M_1 is provided so that simultaneous observations can be made of the motions of the two membranes M_1 and M_2 . The values of these two motions make it possible to determine the phase of the eardrum impedance. For more precise measurements, however, a Wheatstone bridge method is recommended.

MEASUREMENTS OF ACOUSTIC IMPEDANCE WITH THE WHEATSTONE BRIDGE*

The acoustic bridge shown in Fig. 4-39 consists of two capillaries R_1 and R_2 , each connected to a cavity V_1' and V_2' . These two capillaries are connected through a fluid filter system to a pump that produces variations of air pressure. If V_1' and V_2' have the same volume, there will not be any pressure difference between them, and the membrane M will not move. This membrane, which carries a small mirror on which a light beam impinges, is an indicator corresponding to the galvanometer in Fig. 4-40.

The meatus and eardrum are connected to V_1' in the manner described earlier (page 69). The elastic component of the impedance (the compliance) can be balanced by adjusting the volume V_1 with a plunger. The mass or frictional component is balanced by varying volume V_2 . As it is not easy to vary the length of a capillary, its value R is kept constant. However, its influence is altered according to the distribution of the elastic part of the impedance between V_1 and V_2 . If V_2 is increased and therefore V_1 is decreased, the friction R is increased. If $V_2 = 0$, the friction R is without effect. As before (page 69) it is desirable to make the lumen of the capillary so small that Poiseuille's law holds for the air flow at the frequencies of interest. Here the radius $r = 0.238$ mm and the length $l = 2$ cm. Therefore the impedance

$$R = \frac{8\mu l}{\pi r^4} = 3000 \text{ cgs units} \quad (4-4)$$

where μ is the frictional coefficient of air. From Eqs. (4-3) and (4-4) and Fig. 4-40 the impedance at the opening of the meatus can be calculated. The volume of the meatus is subtracted from V_1 to obtain the impedance of the eardrum.

* Extract from Art. 22 as listed in the Author's Bibliography. Published in 1936.

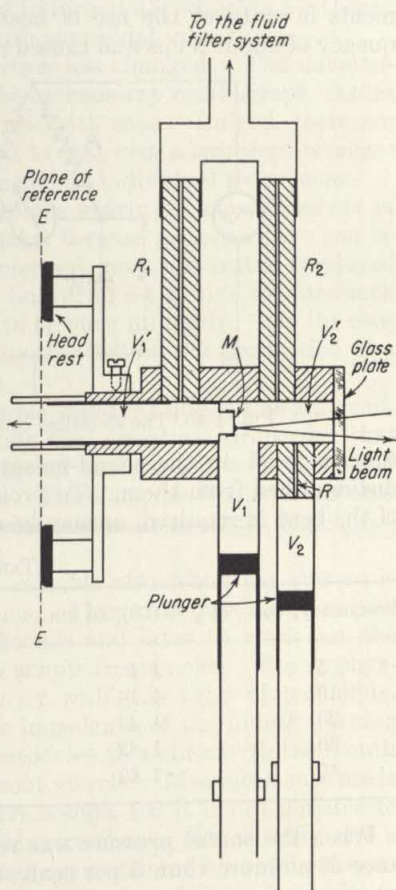


FIG. 4-39. Acoustic bridge for impedance measurements.

For a sound pressure of 10^3 dynes per sq cm the average values obtained are shown in Table 4-3. For frequencies above 10 cps the impedance could be determined with a precision of a few per cent by measuring the amplitude of deflection of the light beam on the manometer membrane. For lower frequencies, however, the results were disturbed by head movements in spite of the use of headrests. These movements had a frequency of about 3 cps and caused changes in the volume of V_1' that were

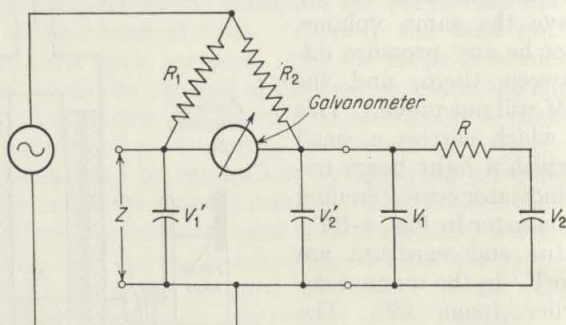


FIG. 4-40. The electrical counterpart of the acoustic bridge.

superimposed on the sound-pressure variations and often could not be distinguished from them. To avoid this difficulty a further stabilization of the head is required, as may be obtained by the use of a biting board.

TABLE 4-3

Frequency, cps	$(V_1 - 0.9)$, cu cm	V_2	Impedance, cgs units
5	1.1	1.87	$(2.23 - 20.9i) \times 10^3$
10	1.14	1.34	$(1.9 - 13.5i) \times 10^3$
20	1.42	0.77	$(0.89 - 8.3i) \times 10^3$
30	1.42	0.69	$(0.82 - 5.8i) \times 10^3$
40	1.62	0.57	$(0.50 - 4.2i) \times 10^3$

When the sound pressure was reduced there was a change of impedance of no more than 5 per cent. A change of this order was observed on stimulation of the opposite ear with a tone of 1000 cps at a pressure of 10 dynes per sq cm. This strong tone produces a contraction of the tensor tympani muscles of both ears, with a stretching of the eardrum and an increase in its impedance.

MEASUREMENT OF TRANSMISSION CHARACTERISTICS AND IMPEDANCES BY THE SINGLE-PULSE METHOD*

Since the establishment of Fourier's principle that any sort of vibration may be regarded as the sum of a series of sinusoidal components, it has been customary to characterize a transmission system in terms of the

* Art. 28 as listed in the Author's Bibliography. Published in 1937.

amplitude and phase changes that it introduces during the propagation of various sinusoidal frequencies within its range. This procedure has been developed to the point where it includes nearly all of the measurements made in acoustics and public-address techniques. The transient responses of a system, though equally good in representing its characteristics, have been difficult to record and to formulate, whereas a-c theory provides simple methods for dealing with sinusoidal vibrations.

During the last few years this situation has changed. The development of oscillographs, and especially the cathode-ray oscillograph, makes it possible to observe transient processes with ease. Indeed, there are situations in which it is more convenient to deal with a transient response than to carry out a series of measurements on individual frequencies.

For example, in the region below 20 cps nearly all measurements of sinusoidal vibrations are difficult to make, because no generators can be found that are free of overtones. Moreover, most apparatus employed for these frequencies is inconveniently bulky; an a-c bridge requires such large inductances and capacitances as to be most unhandy. On the contrary, it is easy to record the transients that follow the production of a shock in such a low-frequency system.

The situation is similar when no simple standard quantities are available. Thus it is not possible to isolate the acoustical properties that correspond to the electrical quantities of resistance, induction, and capacity for a wide frequency range. Therefore, as Schuster pointed out, it becomes necessary to use special norms in acoustic impedance measurements.

The transient method is especially valuable also when the system is available for study for only a short time. Then it is possible to reduce the time of measurement to a few seconds and later to work out the behavior of the system in response to simple frequencies. Many physiological measurements are possible only with this type of technique. For example, the study of the acoustic impedance of the mouth opening is easily carried out by recording the responses to a click with the mouth formed for the production of the different vowels. Measurements made with pure tones give less comprehensive results, for it is not possible to hold the mouth in any one position for more than a few seconds, and a complete determination of the resonance curve cannot be obtained even with automatic recording equipment.

If the pulse technique is repeated periodically it is easy to follow the course of changes in a varying system and to work out the frequency analysis later. The changes of sound transmission in the open air as produced by the wind can be followed in this way, by the oscillographic recording of a series of clicks. In the investigation of sound transmission over great distances a sharp detonation is the simplest acoustical sound source because it can be produced at great intensity and is radiated in all directions. The method is also the most suitable for the study of ground vibrations, for only by setting off an explosive charge can a large enough vibration be produced in the earth to permit measurements of the spread of the waves of different frequencies in the surrounding areas.

Even in the routine testing of communications systems the pulse method is often the most suitable, because continuous observation of the transients may be made on a cathode-ray oscillograph. Then if there is any change in the system it is more readily recognized than when the usual method is used, in which the amplitude transmission for different frequencies is measured, without regard to phase relations. Waetzmann in 1913 showed that the main characteristics of the behavior of a loud-speaker diaphragm could be found by its response to a sudden shock. Also in medical acoustics the percussion methods have been used for a long time.

Calculation Methods. If in a linear transmission system the voltage or

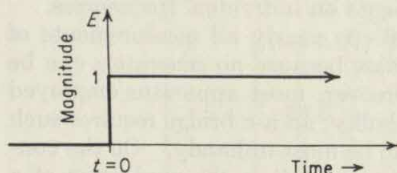


FIG. 4-41. A simple step process.

force of a variable E is zero up to a time $t = 0$ and then suddenly jumps to a unit value and remains there, as seen in Fig. 4-41, a transient vibration arises in a second variable I whose temporal course can be represented as $A(t)$. If this transient vibration $A(t)$ is known, then,

as Carson has shown, the transient vibration $I(t)$ can be found for any sort of temporal variation $E(t)$ arising at $t = 0$, by the formula

$$I(t) = A(0)E(t) + \int_0^t A'(\tau)E(t - \tau) d\tau \quad (4-5)$$

$$I(t) = E(0)A(t) + \int_0^t E'(\tau)A(t - \tau) d\tau \quad (4-6)$$

where the primes represent differentiation with respect to time or $A'(t) = dA(t)/dt$.

If now the variable E begins to undergo sinusoidal vibrations at time $t = 0$ at the frequency $\omega/2\pi$, or $E(t) = E \sin(\omega t + \Omega)$, then I will produce sinusoidal vibrations also, and at the end stage as $t \rightarrow \infty$ the value from Eq. (4-5) is

$$I = E \sin(\omega t + \Omega) \left[A(0) + \int_0^\infty \cos \omega \tau A'(\tau) d\tau \right] - E \cos(\omega t + \Omega) \int_0^\infty \sin \omega \tau A'(\tau) d\tau \quad (4-7)$$

Substituting in Eq. (4-6) we obtain

$$I = E \cos(\omega t + \Omega) \omega \int_0^\infty \cos \omega \tau A(\tau) d\tau + E \sin(\omega t + \Omega) \omega \int_0^\infty \sin \omega \tau A(\tau) d\tau \quad (4-8)$$

if it is assumed that $A(t) = 0$ when $t = \infty$. This assumption, which can nearly always be made in acoustics, means that a d-c change in one variable will not be transmitted to the other. However, if the d-c change produces an alteration of the equilibrium position, the calculations will have to be made by means of Eq. (4-7).

We obtain for the transmission characteristics in the steady state

$$Ie^{i(\omega t + \Omega)} = \dot{U} E e^{i(\omega t + \Omega)} = [\alpha(\omega) + i\beta(\omega)] E e^{i(\omega t + \Omega)}$$

and hence $I = E[\alpha(\omega) \sin(\omega t + \Omega) + \beta(\omega) \cos(\omega t + \Omega)]$

A comparison with Eq. (4-7) gives for the required transmission characteristics

$$\alpha(\omega) = A(0) + \int_0^\infty \cos \omega \tau A'(\tau) d\tau \quad (4-9)$$

$$\beta(\omega) = - \int_0^\infty \sin \omega \tau A'(\tau) d\tau$$

and by comparison with Eq. (4-8) we obtain

$$\begin{aligned} \alpha(\omega) &= \omega \int_0^\infty \sin \omega \tau A(\tau) d\tau \\ \beta(\omega) &= \omega \int_0^\infty \cos \omega \tau A(\tau) d\tau \end{aligned} \quad (4-10)$$

Because E and I are arbitrary variables, they can represent the input voltage and input current of an electric network. Therefore $\dot{U}$ represents the reciprocal value of the impedance. The same holds for the mechanical and acoustical analogies.

The foregoing integrals have exactly the same form as the Fourier integral representing the frequency analysis of an aperiodic vibration, beginning at $t = 0$ and slowly decreasing. This integral is

$$f(x) = \int_0^\infty \cos(\omega x) \varphi_1(\omega) d\omega + \int_0^\infty \sin(\omega x) \varphi_2(\omega) d\omega \quad (4-11)$$

$$\varphi_1(\omega) = \frac{1}{\pi} \int_0^\infty \cos(\omega x) f(x) dx$$

$$\varphi_2(\omega) = \frac{1}{\pi} \int_0^\infty \sin(\omega x) f(x) dx$$

where $[\varphi_1(\omega)^2 + \varphi_2(\omega)^2]^{1/2}$ is the amplitude in the spectrum of the function $f(x)$ for angular frequency ω .

The determination of the transmission characteristics from the transient processes then is of value only if the Fourier integral can readily be evaluated.

Determination of the Fourier Integral. Gray and Bush designed special instruments called integragraphs for the evaluation of integrals of the form

$$f(t) = \int_a^t z(t \pm \lambda) g(\lambda) d\lambda$$

Because they are designed for the most general application they are very complicated, and for our purposes it is better to use a special form.

Practically any harmonic analyzer with a continuously changing base length can be used. If the curve to be analyzed extends from zero to some value, and a base length a is chosen that is longer than this, as

shown in Fig. 4-42, the analyzer gives the integral

$$\int_0^a \cos\left(\frac{2\pi n}{a}x\right) f(x) dx$$

or

$$\int_0^a \sin\left(\frac{2\pi n}{a}x\right) f(x) dx$$

which can be extended to infinity because beyond a , $f(x) = 0$. If we substitute $\omega = 2\pi n/a$ in Eq. (4-11), then by a continuous extension of

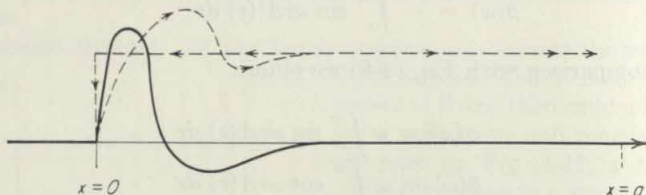


FIG. 4-42. The frequency analysis of a unitary process by means of a harmonic analyzer.

the base length the integral is obtained for various values of ω . In general it is convenient to decrease a to half its length, then jump to its original length, and thereafter to double n . Then each adjustment of the analyzer will give an octave of the frequency range that can be repeated.

If only the amplitude characteristics are of interest it is permissible to displace the curve along the x axis. When phase relations must be determined also this is not possible.

Frequency Analysis of Single Pulses with Mader's Analyzer. Mader's analyzer is the simplest and most generally applicable among those with variable base length. Figure 4-43 presents it in a vertical section. A movable angle piece W carries on its right side a rotatable arm A with a pointer F . A rotation of the pointer turns a gear D on a rack Z . The gear has two depressions, C and S . When the pointer of a planimeter

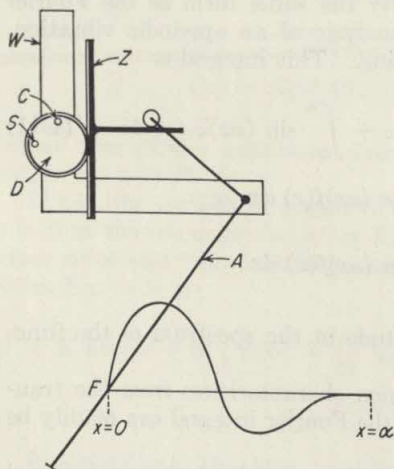


FIG. 4-43. Mader's harmonic analyzer.

is placed in these depressions and F is traced along the curve to be analyzed and back along the x axis, the planimeter surface F_c or F_s is given as

$$\begin{aligned} F_c &= \frac{2K}{a} \int_0^a \cos(\omega x) f(x) dx \\ F_s &= \frac{2K}{a} \int_0^a \sin(\omega x) f(x) dx \end{aligned} \quad (4-12)$$

Here K is a constant of analysis.

Then Eq. (4-11) gives for the amplitude spectrum

$$\varphi_1(\omega) = \frac{aF_c}{2\pi K} \quad \text{and} \quad \varphi_2(\omega) = \frac{aF_s}{2\pi K}$$

when the angular frequency $\omega = 2\pi n/a$. Here ω is expressed as 1/cm. To obtain the usual angular frequency, this value is multiplied by p when the paper speed in the oscillographic recorder is p cm per sec.

Gears are available for the analyzer to give successive values for n of 1, 2, 4, and 8. The length of the curve to be analyzed is conveniently chosen as about 9 cm, so that a is enlarged from 9 to 36 cm by shifting the pointer F along the arm A , whereby a frequency range of five octaves may be covered. To enlarge this range further a second gear is provided with $n = 8$ on whose shaft a gear with $n = 2$ is fastened, and this accessory may be used to enlarge the ratio by engaging the gears $n = 4$ or $n = 8$. Then the constant K of the analyzer is enlarged fourfold and n becomes 16 or 32, so that seven octaves can be covered.

In this manner it is possible to make measurements up to the 32nd overtone of the base length. If it is desired to go still higher, then the integral is separated into partial integrals

$$\int_0^\infty = \int_0^a + \int_a^{2a} + \cdots + \int_{(n-1)a}^{na}$$

That is to say, the curve to be analyzed is taken as longer than 9 cm and is integrated by parts until $f(x) = 0$, and the partial values obtained for F_c and F_s are added.

In carrying out the analysis it is convenient to fasten the curve to be analyzed on a carriage that may be moved along the x axis, so that without any shifting of the analyzer for different base lengths it is always possible to place the various intersecting points of the curve at the start of the base line.

If the curve to be analyzed does not approach the base line as time increases, but instead approaches a constant value e , as indicated by the dotted line of Fig. 4-42, the pointer of the analyzer is not brought back to the x axis but to the level of the dotted line. To obtain the amplitude spectrum of $f(x)$ it is necessary to add to the value obtained for $\varphi_2(\omega)$ the amplitude spectrum of the backward-running rectangular curve represented by $\varphi_2'(\omega) = e/(\pi\omega)$.

Determination of the Frequency Response of a Transmission System with Mader's Analyzer. If the differential of the transient $A(t)$ produced by a sudden step is known, a comparison of Eqs. (4-9) and (4-12) for the transfer function measured with Mader's analyzer gives

$$\alpha(\omega) = A(0) + \frac{aF_c}{2K}$$

$$\beta(\omega) = -\frac{aF_s}{2K}$$

On the other hand, if the transient for the sudden step itself is given, then by Eq. (4-10)

$$\alpha(\omega) = \frac{n\pi F_s}{K}$$

$$\beta(\omega) = \frac{n\pi F_c}{K}$$

where $\omega = 2\pi n/a$ is again measured in 1/cm and is to be multiplied by p if the oscillographic trace represents the transient of the paper speed in p cm per sec.

To obtain an indication of the precision of this method of integration, the loading current of a condenser of $C = 1\mu\text{f}$ connected in series with a

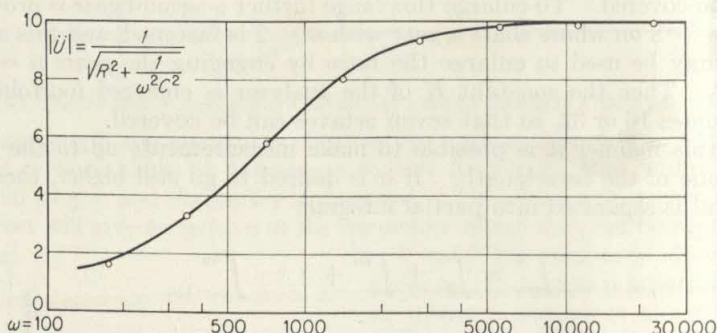


FIG. 4-44. The curve represents the transmission characteristic as calculated from the a-c impedance, and the points represent this characteristic calculated from the observed transients. The abscissa represents angular frequency ($\omega = 2\pi f$) and the ordinate the transmission characteristic.

resistance $R = 1000$ ohms was determined for a suddenly applied voltage. The absolute value of the transient, *i.e.*, the reciprocal of the impedance, is $|\dot{U}| = [\alpha(\omega)^2 + \beta(\omega)^2]^{1/2}$. The observed values are shown by the points in Fig. 4-44, whereas the curve represents calculated values according to the formula

$$\frac{1}{Z(\omega)} = \frac{1}{R + 1/i\omega C}$$

It is clear that the observed and calculated values agree within 1 per cent.

Sources of Pulses. For precise measurements of transients it is necessary to employ pulses of simple form. In electrical systems such pulses arise from the sudden introduction of a d-c voltage. A rectangular voltage pulse also can be used, and if its duration is dt , the transient process is $E[A(t) - A(t - dt)] = EA'(t) dt$, and so Eq. (4-9) can be used. It is necessary that dt be small relative to the period of the frequencies that arise, and therefore this method is especially suitable for systems with low natural frequencies. In such systems a mechanical relay can be used to produce the pulse. For higher frequencies use may be made of either electrical relays or the arrangement used by Wagner (3) for the pro-

duction of synthetic vowels, which employs the rectangular form of the hysteresis loop produced in a magnetic alloy when exposed to a sudden change of inductance. From the calculations made by Wagner on the spectra produced by pulses of various forms it is possible to evaluate the errors that arise when the test pulses are insufficiently brief.

For sound transmission in air and for most acoustic systems only short pulses can be employed. The sound of an electric spark is a satisfactory source. To obtain large sound pressures a Leyden jar or a static machine may be used, and for ordinary sound pressures the arrangement shown in Fig. 4-45 is satisfactory. It consists of an injection needle *T* with a short tube attached, and at the end of the tube a graphite rod (the lead

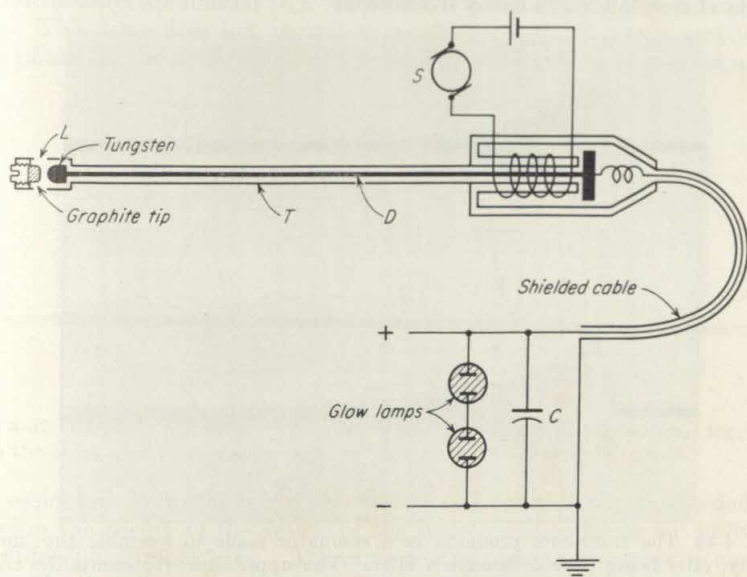


FIG. 4-45. A spark apparatus.

of a hard-grade pencil). Within the needle is an insulated wire *D* with a tungsten contact at one end and the armature of a relay at the other end. The relay is damped by layers of rubber. When switch *S* is closed, the armature is pulled in and the tungsten tip brought in contact with the graphite rod, producing a discharge of condenser *C*. The same switch operates an oscillograph. The sound produced by the spark is transmitted to the air through holes *L* in the tube surrounding the graphite rod. The tip and injection needle are grounded, and the whole apparatus is electrically shielded. This method has served for measurements of the resonance of the mouth cavity, and the device can even be placed far back in the throat. Sparks of a suitable intensity were produced over a period of several months without any difficulty.

For producing shocks in a small mechanical system the hammer of a piano was used.

Examples of the Application of the Shock Method. Two examples from physiological acoustics will serve to illustrate the suitability of the method. Cotton studied models to obtain information on the effects of stiffness of the walls of the mouth on speech. He constructed cylindrical resonators with walls of fresh meat and water-soaked cotton. The resonance curve was determined by observing the increase in sound pressure that occurred when the resonator was placed in front of the vibrating loudspeaker diaphragm. These measurements gave a flat curve and hence were not in accordance with existing theory of vowel production. Control experiments showed that in the repeated placing and removing of the resonator there may be slight alterations of its form in which sharp points of resonance are easily overlooked.

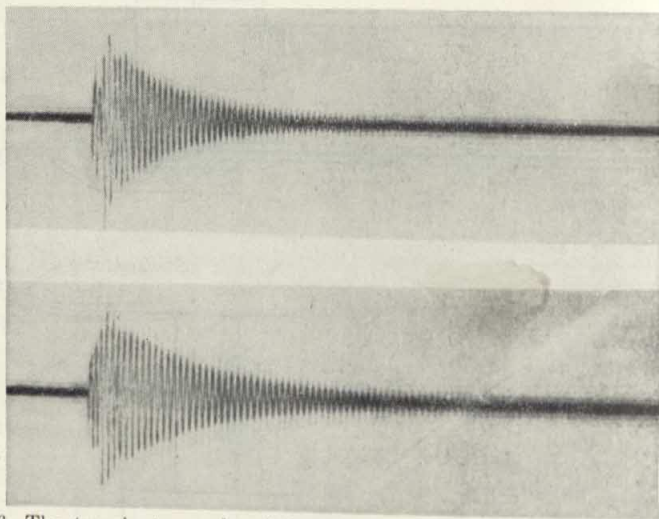


FIG. 4-46. The transients produced in a resonator made to resemble the mouth cavity, after being passed through a filter. The upper curve represents the effects from the resonator alone and the lower curve the effects when it was enclosed in a metal case.

To avoid this difficulty and to reduce the time required for the measurements, the spark producer shown in Fig. 4-45 was placed on the floor of the resonator and the resulting transients were recorded by a condenser microphone located near the opening of the resonator. It was found that a resonator made of water-soaked cotton actually produced nearly aperiodic vibrations. This happened because strands of cotton extending from the surface produced heavy damping. It was the surface roughness and not a compliance of the wall that produced the damping. In the resonators made of meat there were great difficulties in obtaining an impervious surface, and it was found that a barely noticeable opening in the wall had a strong damping effect.

In order to obtain a resonator whose walls had the consistency and surface characteristics of the cheeks it was necessary to use a mixture of glycerin and gelatin, whose formula was 7 grams of gelatin, 42 cu cm of

water, 50 grams of glycerin, and 1 gram of phenol. This material was formed in a metal mold and removed as a tube after gentle warming of the mold. A resonator formed in this way had a length of 15 cm, an inside diameter of 2.5 cm, and a wall thickness of 1.2 cm (corresponding to the cheeks). Its transient vibrations after passing through an octave filter had the form shown in the upper portion of Fig. 4-46. The lower portion of this figure shows the response of the same resonator still in its metal form. The close similarity of the two curves shows that yielding of the walls can have little effect upon the resonance of the mouth cavity.

The second example has to do with the transmission characteristics of the ossicles of the middle ear, measured in the fresh cadaver. Such measurements are limited to a few hours after the removal of the middle ear. This time does not permit measurements of vibratory amplitude and phase for the whole range of frequencies at all points of interest along

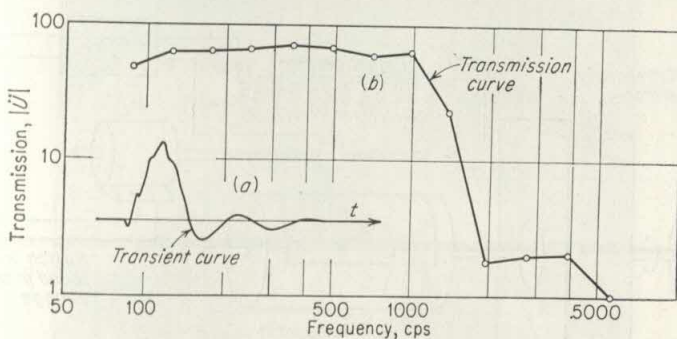


FIG. 4-47. Transient vibrations produced by the manubrium of the malleus, together with the calculated transmission curve of the system meatus-manubrium.

the ossicular chain, though such extensive measurements are needed to develop the theory of the action of the system and to bring out individual differences among ears. Attempts to study the movements by means of small mirrors or aluminum particles on the surface led to uncertain results, because in the long times required for this procedure these small bodies shifted their locations.

However, if the eardrum was exposed to a sharp click and the rotary movements of the handle of the malleus were recorded by means of a mirror, a transient was obtained as shown by curve *a* of Fig. 4-47. Then by Eq. (4-9) a calculation was made of the transmission characteristics, as shown by curve *b* of this figure. By this procedure the preparation was conserved and the measurements were carried out in a short time.

A NEW AUDIOMETER*

An audiometer was designed in which the intensity of the tone increases continuously as long as a signal button is pressed and decreases as long as this button is released. The subject thus can cause the intensity of

* Article 49 as listed in the Author's Bibliography. Published in 1947.

the tone to fluctuate between just above and just below threshold. The amplitude of these fluctuations is a measure of the difference limen for intensity, which is automatically recorded together with the absolute threshold. The magnitude of the difference limen may be used to decide whether a hearing loss is due to a conductive or to a perceptive lesion.

The instrument includes a noise for masking the ear that is not being tested. This is usually essential, especially in measurements by bone conduction, and it is helpful also to vary the intensity of the test tone. An automatic arrangement is provided for this purpose, and by this means the masking noise is delivered at a strength sufficient to exclude the unwanted ear without being so strong as to diminish the acuity of the ear under test.

Requirements of an Audiometer. In audiometric measurements sounds should be avoided that are appreciably louder than threshold because

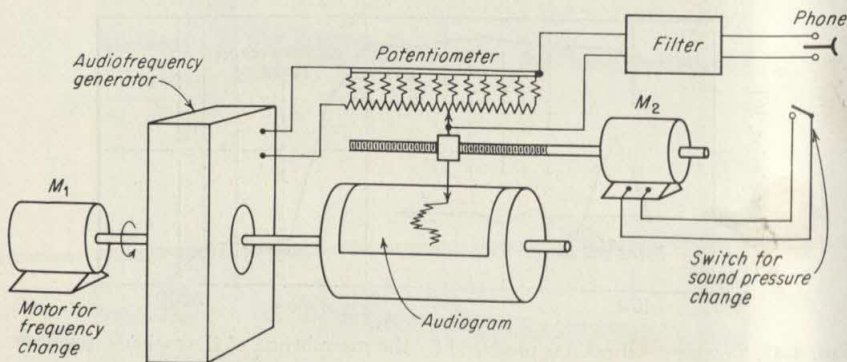


Fig. 4-48. Schematic diagram of the audiometer.

they cause fatigue and make the determinations erroneous. Moreover, the measurements need to be carried out as rapidly as possible so that the attention will be maintained at an effective level. The conventional method, in which the test tone is increased in a number of steps beginning below threshold, is unnecessarily time-consuming, because many of the judgments are not determinative. In the ideal audiometer the test tone is always close to the threshold.

Principle of the New Audiometer. As just described, an audiometer was constructed in which the intensity of the test tone increases continuously as long as a button is pressed and decreases continuously as long as it is not pressed. The subject holds the button down until the tone becomes audible, then releases the button until the tone disappears, presses again until the tone reappears, and so on. Thus the tone fluctuates about the threshold all the time, and the amplitude of this fluctuation is a measure of the difference limen for intensity at the absolute threshold. Both of these thresholds are automatically recorded.

The arrangement of the apparatus is indicated schematically in Fig. 4-48, and a photograph is shown in Fig. 4-49. A motor M_1 produces a continuous change in the frequency of the audio-oscillator. The whole

range between 100 and 10,000 cps is covered in 15 min. On the same shaft as the motor is a drum holding a card on which the sound intensity is recorded by a stylus. The oscillator works into a potentiometer that covers a range of 140 db and connects with the telephone receiver. A second motor M_2 controls the position of a sliding contact on this potentiometer and at the same time moves the stylus. This second motor is under the control of the subject. When he pushes the signal button the contact moves to the left and the intensity in the telephone receiver

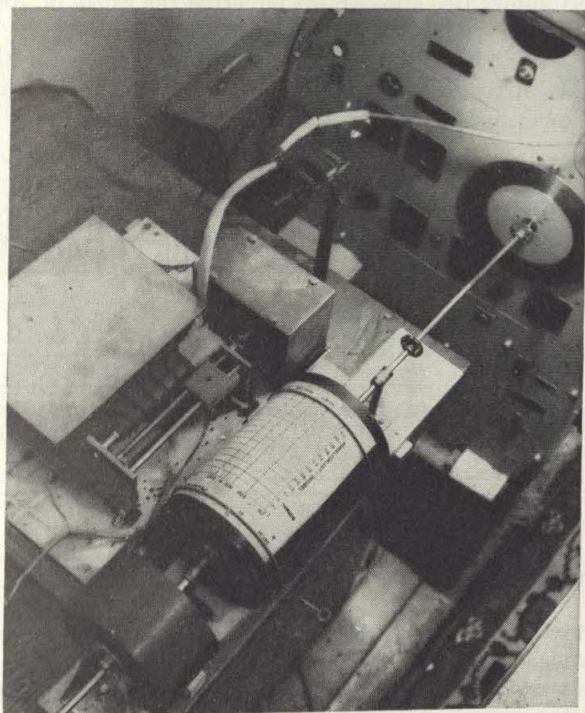


FIG. 4-49. Photograph of the audiometer.

increases. When he releases the button the motor is reversed, the contact moves to the right, and the sound intensity decreases.

The potentiometer could be constructed so as to give a continuous variation of intensity, but in order to give high reliability it was arranged to provide stepwise changes of 2 db. At high intensities a slight click is heard as the slider moves from one step to another, but this transient is inaudible near the threshold.

To make the normal audiogram a straight line a corrective network was introduced between the potentiometer and the receiver. This network provided large attenuation for frequencies between 1000 and 3000 cps and also reduced the magnitude of the transients.

Reproducibility of the Threshold Measurements. To test the reproducibility of the threshold, steady tones of 200 and 10,000 cps were

observed for a period of 15 min. The audiograms in Fig. 4-50 show that the variations over this period of time occurred usually at a slow rate and had a magnitude of about 5 db. They sometimes were larger at 10,000 cps because of shifts in the position of the receiver on the ear, which altered the resonances. Such shifts could be produced by movements of the lower jaw. The difference limens as indicated by the up-and-down fluctuations are highly regular, and there have been no complaints of fatigue on the part of subjects, even after tests lasting an hour.

Figure 4-51 shows two audiograms covering the range of 100 to 15,000 cps, representing successive tests on an untrained subject. The reproducibility is less above 5000 cps because the resonances of the receiver and meatus are altered when the receiver is taken off the ear and replaced. These resonances are sharp, and the audiogram may differ slightly if at

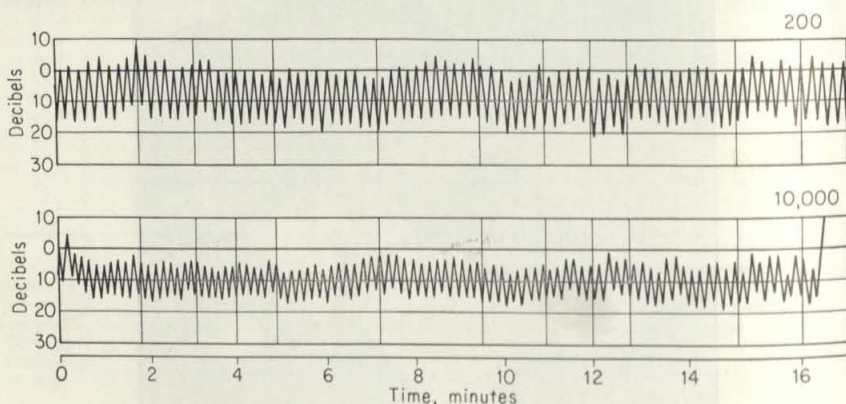


FIG. 4-50. Responses to steady tones of 200 and 10,000 cps, observed over a period of several minutes.

one time they are traversed with the intensity rising and at another time with the intensity falling.

The effect on the threshold of the rate of change of intensity was studied, with results indicated in Fig. 4-52. This rate at first was 90 db per min, and then it was changed suddenly to 220 db per min. The absolute threshold was not affected, but there was an increase of the difference limen.

A tone of threshold intensity requires about 0.5 to 1.0 sec in order to reach its full loudness, and the reaction time for pressing a key is about 0.2 sec. To avoid mechanical delays a microswitch was used as the signal button, for a movement of 0.2 mm was sufficient to operate it. It was further necessary to use a rotor of low inertia in the motor M_2 so that a reversal of direction could occur with minimum lag. It would also be possible to use a reversible transmission and to keep the motor running continuously.

The rate of change of intensity must not be too small, because the details of the audiogram are then obscured. In preliminary tests a rate of change of 140 db per min was used. The subject's task of pushing the

button is a rhythmic one. There is a risk, therefore, that he will be guided by his sense of time instead of his threshold. The following experiment was carried out to test this possibility. At a given moment, indicated by the arrow in Fig. 4-53, the oscillator current was turned off

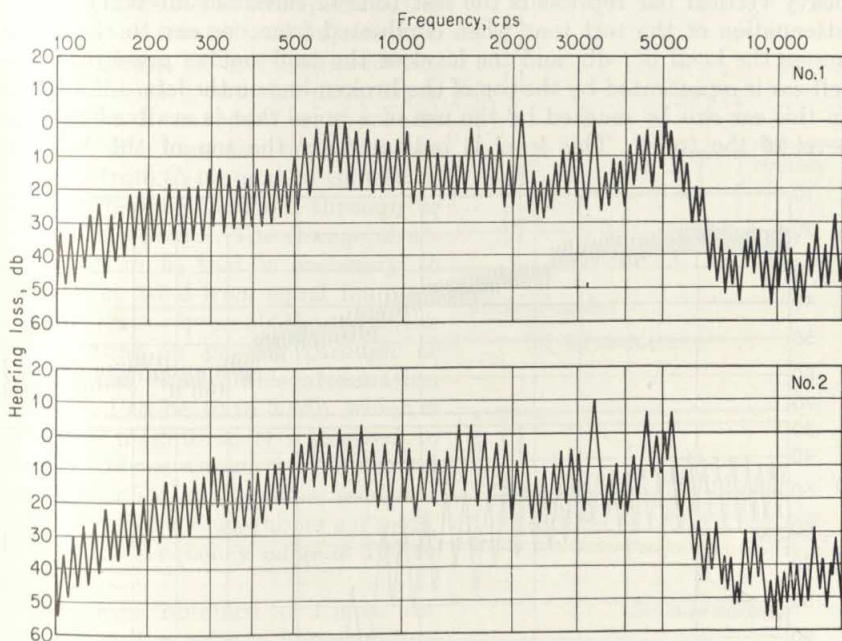


FIG. 4-51. Successive audiograms obtained on an untrained subject.

and the subject was asked to continue to press the button in the same rhythm as before. He could guide his behavior by the rhythm of the heart, or by breathing movements, or by a sense of musical rhythm. These alternatives gave different kinds of curves. If the breathing movements were used there were sudden displacements of the curves as

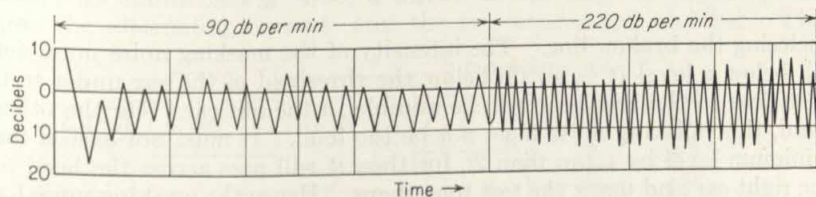


FIG. 4-52. Effect of a sudden alteration of the rate of change of intensity from 90 db per min to 220 db per min.

shown in *a* of Fig. 4-53. If a pure time sense was relied upon the amplitude of the fluctuations waxed and waned as shown in *b* of this figure, while the level of the curve usually deviated toward higher or lower values. After some experience these curves are usually easy to diagnose, for they have a different character from true audiograms.

Masking the Other Ear. The relations obtaining in the measurement of air-conduction thresholds are indicated in *a* of Fig. 4-54. The ear being tested (right ear) is represented on the right and the other ear, which is to be masked, is represented on the left. The height of the heavy vertical bar represents the test tone of threshold intensity. The attenuation of the test tone when conducted from one ear to the other across the head is t db, and the level of the test tone as present in the left ear is represented by the top of the broken-line on the left. The tone in this ear can be masked by the use of a noise that is m db above the level of the tone. This level is indicated by the top of the bracket

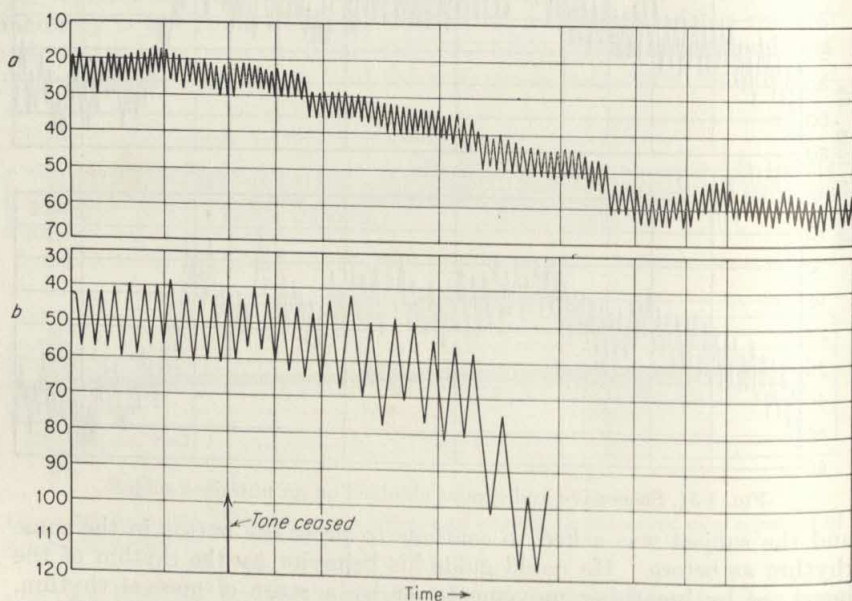


FIG. 4-53. Rhythmic pressings of the button after the tone was turned off. For curve *a* the subject relied upon his breathing movements, and for curve *b* simply upon his time sense.

enclosing the broken line. The intensity of the masking noise must not fall below a level $(t - m)$ db below the threshold of the ear under test. If it does so the test tone will be audible in the left ear. On the other hand, this masking noise must not be too loud. It must not exceed the minimum level by more than $2t$, for then it will pass across the head to the right ear and mask the test tone there. Hence the masking noise for air-conduction testing must be held within a range of intensity of $2t$ db.

For bone conduction the situation is different. There is no attenuation of the test tone from one ear to the other, and in fact the tone may be heard better in the wrong ear. Therefore the masking noise has to be kept within an interval of intensity less than t db, as the diagram shows.

The attenuation of an air-conducted tone from one ear to the other

may be measured by the method of best beats, as used by Lane and illustrated in Fig. 4-55. Oscillator G_1 produces a loud tone in the receiver on the left, and G_2 produces a tone in the receiver on the right. The frequency from G_2 differs from that from G_1 by 1 cps. By means of the switches and attenuators b_1 and b_2 the tones are alternated and adjusted to equal loudness. Then both tones are sounded at once, and that from G_2 is reduced until maximum beats are obtained. The maximum appears when the tone from G_2 is equal to that from G_1 after being conducted through or around the head. The change of attenuation in b_2 that is necessary to reduce the tone from equal loudness to best beats represents the reduction of the tone in passing through or around the head. This attenuation was found to be 40 to 50 db, which is thus the magnitude of t referred to above. These values were obtained for a number of dynamic receivers provided with sponge-rubber ear pads, and for the frequency range of 100 to 10,000 cps.

The value obtained for t is so low that difficulties arise in bone-conduction measurements if the intensity of the masking noise is not adjusted to the intensity of the test tone. This adjustment can be made with a second potentiometer that is mechanically coupled to the first one. Another method is to use the same potentiometer for both tone and noise. As shown in Fig. 4-56, a direct current may be superimposed upon the alternating current, and the two attenuated together. The

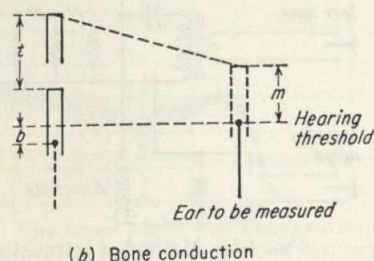
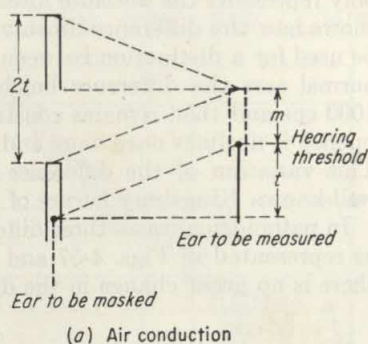


FIG. 4-54. Diagrams to show intensity relations of the masking tone for air and bone conduction.

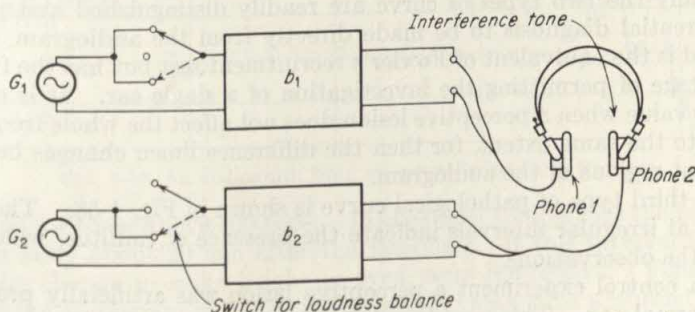


FIG. 4-55. Circuit for measuring the attenuation from one ear to the other by the best-beats method.

attenuated direct current then can be separated from the alternating current by means of a filter and chopped by means of an interrupter to produce the masking noise.

Audiograms for Pathological Ears. The new type of audiogram not only represents the absolute intensity as a function of frequency but also shows how the difference limen varies with frequency. These data may be used for a distinction between perceptive and conductive lesions. In normal ears the difference limen increases somewhat between 100 and 1000 cps and then remains constant to about 4000 cps. Above this frequency it declines once more and reaches its original value at 10,000 cps. This variation of the difference limen with frequency agrees with the well-known Kingsbury curves of equal loudness.

In pathological cases three different types of audiogram were obtained, as represented in Figs. 4-57 and 4-58. In the upper curve of Fig. 4-57 there is no great change in the difference limen with frequency, and the

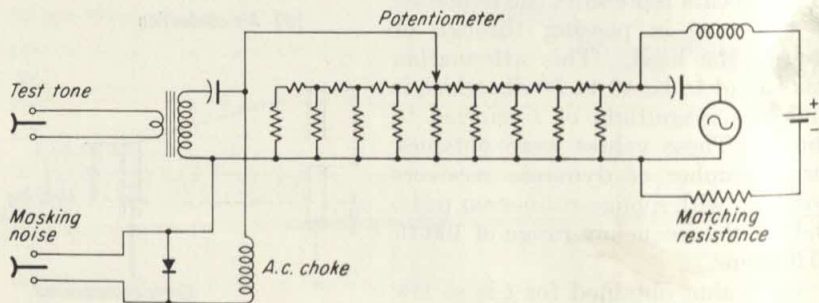


Fig. 4-56. Method of attenuating a tone and a noise at the same time.

curve has the usual form. In the lower curve, however, there is a marked decrease in the amplitude of the intensity fluctuations; the difference limen as measured at threshold declines progressively for the higher frequencies. The upper curve represents an ear that on other grounds was diagnosed as suffering from a conductive lesion. The lower curve represents one that was diagnosed as suffering from a perceptive lesion.

Usually the two types of curve are readily distinguished and permit a differential diagnosis to be made directly from the audiogram. This method is the equivalent of Fowler's recruitment test but has the further advantage of permitting the investigation of a single ear. It is of particular value when a perceptive lesion does not affect the whole frequency range to the same extent, for then the difference limen changes between different regions of the audiogram.

The third type of pathological curve is shown in Fig. 4-58. The large spikes at irregular intervals indicate the presence of tinnitus, which disturbs the observations.

As a control experiment a perceptive lesion was artificially produced in a normal ear. This was done by fatiguing the ear for 10 min with a tone of 1000 cps at an intensity close to the threshold of feeling. The

audiogram as determined after a pause of 10 min is shown in Fig. 4-59. Before the fatiguing the amplitude of the spikes was more than 10 db over the whole frequency range, but after the fatiguing it was markedly

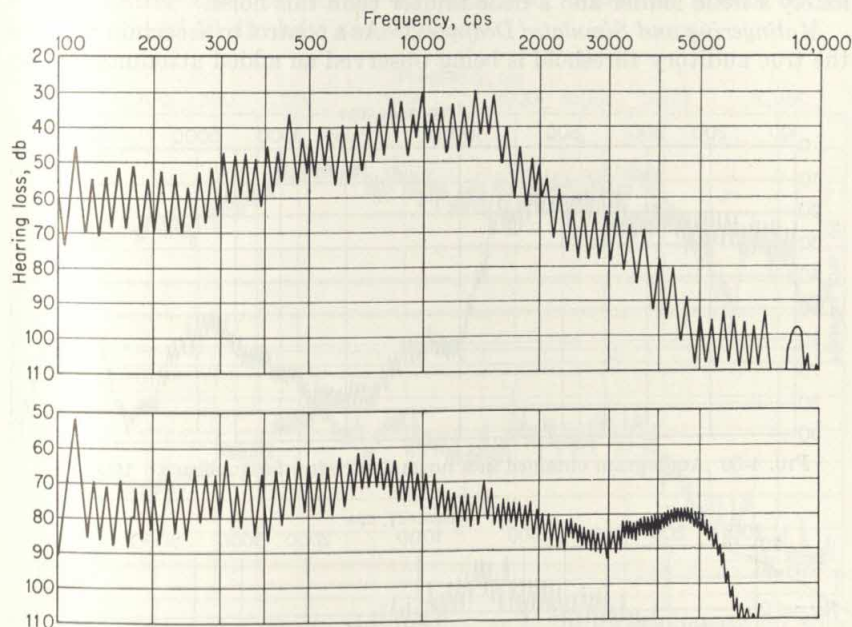


FIG. 4-57. Pathological types of audiogram. The upper curve was obtained from an ear with conductive deafness, the lower one from an ear with perceptive deafness.

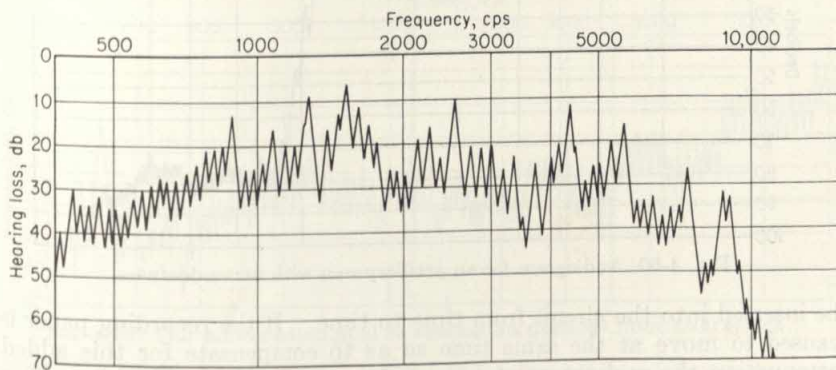


FIG. 4-58. An audiogram from an ear suffering from tinnitus.

reduced for tones above 1000 cps. In the upper frequencies the measurements came about 20 min after the fatiguing. If this interval is made less the change in spike height is even more impressive. Figure 4-60 shows the audiogram obtained for an artilleryman with a normal middle ear and nerve deafness.

In the study of perceptive deafness it often is useful to record curves

of equal loudness. This can easily be done with the new audiometer. A constant noise is presented to the ear that is not being tested and the subject is asked to permit the test tone in the other ear to become alternately a little louder and a little fainter than this noise.

Malingering and Simulated Deafness. As a control to ascertain whether the true auditory threshold is being observed an added attenuation may

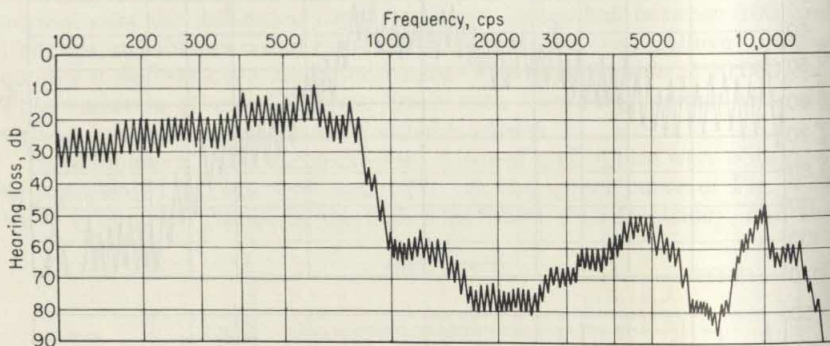


FIG. 4-59. Audiogram obtained in a normal ear after fatiguing with 1000 cps.

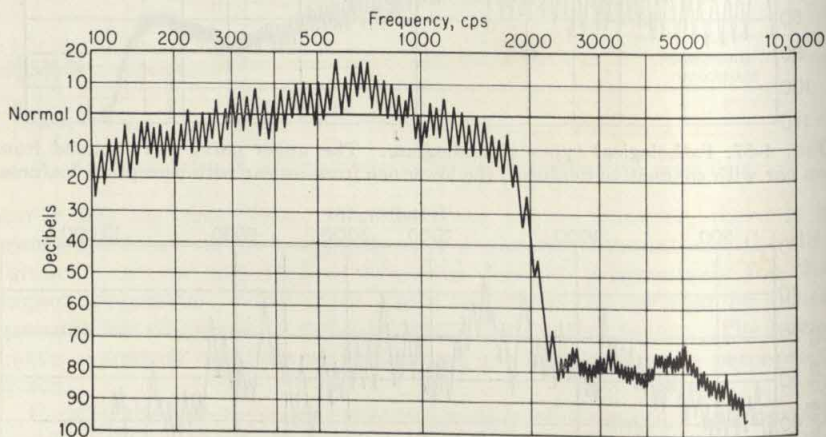


FIG. 4-60. Audiogram for an artilleryman with nerve deafness.

be inserted into the circuit from time to time. If the recording paper is caused to move at the same time so as to compensate for this added attenuation the audiogram of a normal ear maintains a straight course except for a larger spike at the moment that the addition is made. Such an audiogram is shown at the bottom of Fig. 4-61 and may be compared with the usual audiogram above. As the lower curve was obtained an attenuation of 10 db was inserted every 2 min. The two curves are in good agreement except at the beginning for 100 cps, before the subject had settled down, and at the end near 10,000 cps because of a difference in the placing of the receiver on the head.

In malingering, where a true threshold is not obtained, the subject is unable to follow the intensity changes and a peculiar form of curve is recorded. For Fig. 4-62 the subject made an honest effort up to 1500 cps but thereafter tried to conceal his deafness. Here the effects of the introduction of 10 db shifts are obvious.

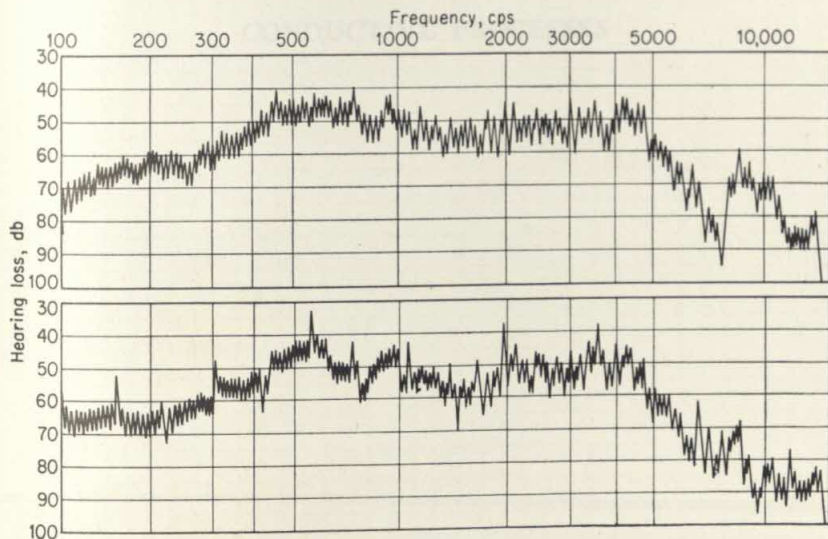


FIG. 4-61. Above, a normal audiogram. Below, an audiogram for the same ear, with 10 db of attenuation inserted every 2 min.

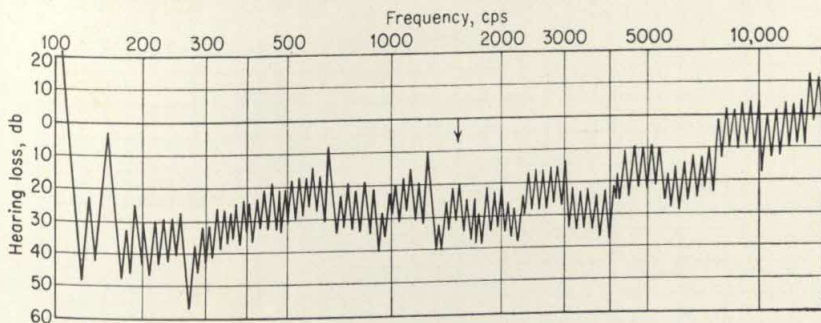


FIG. 4-62. The subject attempted to conceal his deafness from 1500 cps on.

The audiometer was calibrated in absolute units for air conduction. If a completely straight horizontal line is desired for the normal audiogram it will be necessary to compensate for the minor variations remaining after the use of the electric network. This may be done mechanically by having the drum that carries the audiogram card shift along the intensity axis as determined by a profile.

CHAPTER 5

THE ACTION OF THE MIDDLE EAR

MOVEMENTS OF THE AUDITORY OSSICLES*

In architectural acoustics it has been shown that when vibrations are transmitted from a body of low acoustic resistance to one of high acoustic resistance the resulting amplitudes are determined essentially by the pressure existing at the boundary. It can be assumed that the pressure acting on the body of high resistance is not affected by the relatively small amplitudes of vibration of this body, because of the great compliance presented by the body of low resistance. These relations hold for the ear because the air is tenuous, and therefore the ear is essentially a pressure receptor. This matter of pressure transmission is of interest for the ear because the sensitivity can be increased by a pressure transformation.

It is well known that for the high tones in particular the obstacle effect of the head and the resonance of the external meatus bring about an alteration of the sound pressure, so that its magnitude at the eardrum is considerably greater than in the free field. This enhancement of pressure can be calculated† and can readily be measured with a probe in a subject's ear (Kuhl).

Pressure Transformation in the Middle Ear. After the pressure at the eardrum is known, the next step is to discover how it is transmitted to the cochlear fluid. First of all it is important to find to what extent the pressure acting on the total surface of the eardrum is transferred to the manubrium of the malleus, which is attached to the eardrum. After an amplification of about 1.3-fold by the lever action of the ossicular chain, this pressure is applied to the stapes. As the surface of the eardrum is significantly greater than the footplate of the stapes, we expect a considerable increase in the pressure (force per square centimeter) on the footplate.

The Catenary Hypothesis. According to Helmholtz (1,2), a further enhancement of pressure is achieved because the eardrum does not act like a stiff piston carrying the manubrium along as an integral part, but acts in a peculiar way. Its slightly convex form, produced by the fibers running toward the center (the radial fibers), makes it possible for a small force acting at the middle of the fibers to produce a much greater force at the ends of the fibers, in much the same way that a stretched string produces forces on its end supports when its middle is displaced laterally.

* Article 38 as listed in the Author's Bibliography. Published in 1941.

† See Chap. 7, p. 268.

In order for the eardrum to produce a pressure transformation of this sort it is necessary that the radial fibers be inelastic and that the circular fibers be relatively compliant, so that the conical form of the eardrum can be altered. Studies in which small portions of the eardrum were cut out showed that there was actually a difference in the strength of the membrane in the different directions. However, the elasticity in the two directions was of the same order of magnitude. The same is indicated when the normal eardrum is touched with a fine hair. The depressed surface is nearly always completely circular if the tissue is in a fresh condition. On the other hand, a rubber membrane that is stretched unevenly will show an elliptical depression when tested in this manner. Therefore we must not expect to find a greater pressure transformation than is provided by the ratio between the surfaces of eardrum and stapelial footplate.

If we regard the eardrum as a stretched membrane in which the manubrium of the malleus is embedded, then according to the extensive calculations of Frank only a part of the pressure acting on the eardrum will be transferred to the manubrium. Tests were made in which circular stretched membranes similar to the eardrum were provided with a rod extending from one edge to the middle, and with an axis of rotation at the edge. When the membrane was acted upon by air pressure applied to one side, the rod could be brought back to its resting position by applying a force to the center of the membrane which was about one-fourth of the total force applied to the surface of the membrane. If in addition an air cavity corresponding to that of the middle ear was placed behind the membrane, the pressure transfer was still smaller. This happened because the opposing force of the compressed volume of air reduced the effect of the unilateral air pressure.

Measurements of Transformer Action. To measure the pressure transformation in the human ear, the following experiment was carried out in cadaver specimens. A sound pressure was applied through the external meatus and at the same time was opposed by another sound pressure acting on the inner surface of the stapelial footplate, and the amplitude and phase of this second alternating pressure were adjusted so that the stapelial footplate remained at rest. The ratio of these two pressures represents the pressure transformation of the middle ear. A capacitative probe, as described earlier (page 53), was used to show when the stapes was motionless.

In this experiment it was highly important to avoid any drying of the preparation. The footplate of the stapes had to be exposed quickly, and despite the great variability in the form of temporal bones this exposure had to be made so that the probe could be placed in the line of vibration of the stapes. Experience with many specimens showed that it was easiest to expose the stapes by working with a drill from the brain side of the temporal bone, proceeding along the path of the auditory nerve, until finally the thin wall between the internal acoustic meatus and the labyrinth was penetrated (see Fig. 5-1). When the nerve in the internal auditory meatus was removed and the fluid of the labyrinth was sucked

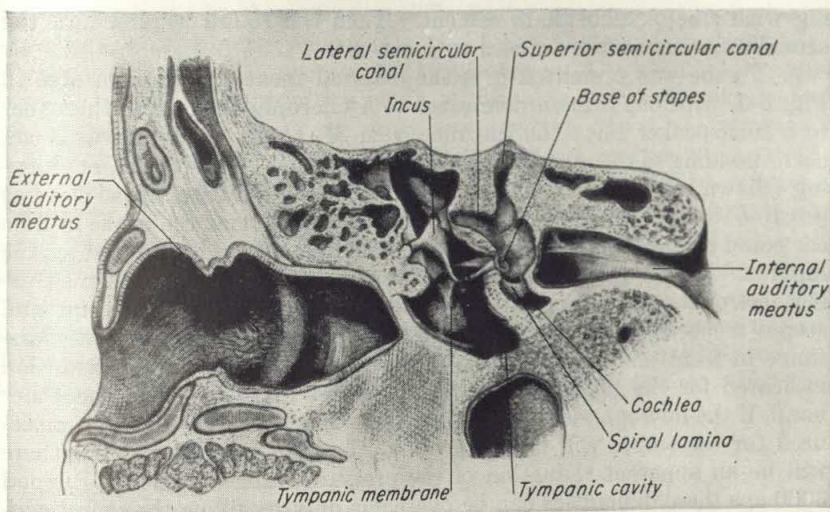


FIG. 5-1. A cross section through the ear showing the simplest way of exposing the stapedial footplate, after Toldt.

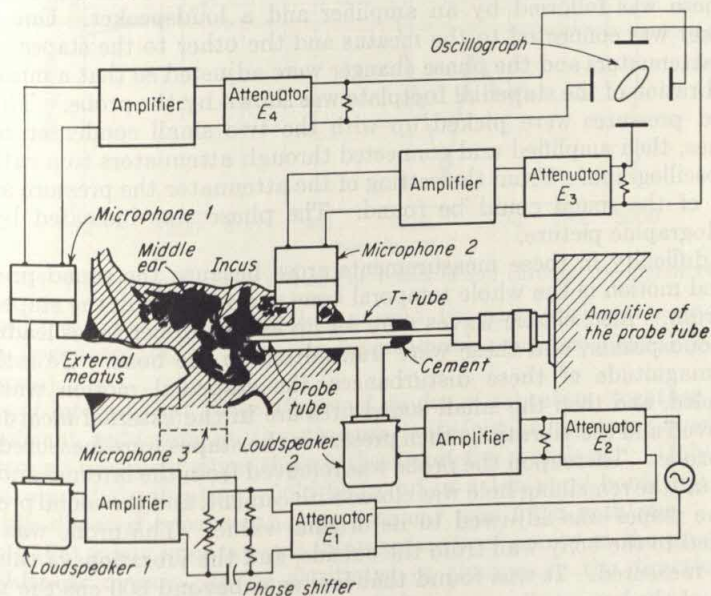


FIG. 5-2. Arrangement for measuring pressure transformation in the middle ear.

out, the footplate of the stapes usually could be seen directly at the end of the opening. No damage was done to the middle ear. After a suitable enlargement of the opening a small brass tube was inserted. As shown in Fig. 5-2, this brass tube was connected to a microphone M_2 and a sound source. The brass tube was cemented into the bony open-

ing with zinc oxyphosphate cement. Then the round window and the semicircular canals were closed with cement.

A T tube was cemented into the external meatus, as shown also in Fig. 5-2, with one branch connected to a microphone M_1 and the other to a loudspeaker L_1 . The distance from M_1 to the eardrum was 3 cm, corresponding to the normal length of the meatus. In addition, an opening (shown by dotted lines) was drilled into the bony meatus as close as possible to the eardrum, so that the pressure transformation of the middle ear could be measured apart from the pressure changes introduced by the meatus. In these measurements it was necessary to have the measuring microphones M_1 and M_2 as close as possible to the eardrum and stapes respectively so as to avoid resonances in the tubes. If the distance in front of the eardrum is too great, the pressure transformation indicated for the higher frequencies becomes excessive. On the other hand, if the microphone M_2 is too far from the stapes, the pressure measured for the stapes will be too great at the high frequencies, and there will be an apparent reduction of the pressure transformation. Beyond 3000 cps these difficulties can be overcome only by filling the sound-conducting tubes with hydrogen.

The audio-oscillator worked into two attenuators E_1 and E_2 , and each of these was followed by an amplifier and a loudspeaker. One loudspeaker was connected to the meatus and the other to the stapes. The two attenuators and the phase changer were adjusted so that a minimum of vibration of the stapedial footplate was shown by the probe. The two sound pressures were picked up with the two small condenser microphones, then amplified and connected through attenuators to a cathode-ray oscillograph. From the setting of the attenuator the pressure amplitude of the sound could be found. The phase was indicated by the oscillographic picture.

A difficulty in these measurements arose because the sound pressure caused motion in the whole temporal bone and not just in the stapes and eardrum. Also, elastic waves were set up in the rubber tubes leading to the loudspeaker, and these were transmitted to the bone. To estimate the magnitude of these disturbances, the stapedial motion was first canceled, and then the small sound pressure in the external meatus was removed and the vibrations then present in the stapes were measured with the probe. Thereupon the probe was removed from the internal auditory meatus, the remaining hole was closed with cement, and the sound pressure at the stapes was adjusted to its original value. The probe was then applied to the bony wall from the outside, and the vibrations of this wall were measured. It was found that for tones beyond 800 cps the vibrations of the bony wall were negligible relative to those of the stapes. At 200 cps, however, these wall vibrations were noticeable as long as the probe was placed loosely against the bone. But if the probe was placed in a lateral position against the wall and fastened with cement these disturbances disappeared, for then the probe vibrated along with the bone. Therefore, care was taken that the probe was securely cemented in. The probe was easily detached from the amplifier, so that even when

it was cemented in there was no difficulty in carrying out preliminary operations on the bone.

It was found best to prepare the probes only a day or so before they were to be used, because in the course of time tiny cracks often appeared in the varnish with which the probe was covered, and in the saturated air within the temporal bone the insulation was gradually impaired.

A study was first made of the pressure transformation in its relations to amplitude. It was shown that for a tone of 200 cps, for example, no overtones were present even when the sound pressure was raised to a high level. But if this pressure was raised further and exceeded a certain value, there was a sudden appearance of overtones. Then, for example, an increase in amplitude of 30 per cent might increase the overtones from 1 per cent to 8 per cent. By listening it was easy to note that this sudden increase of overtones occurred around the threshold of feeling, when the

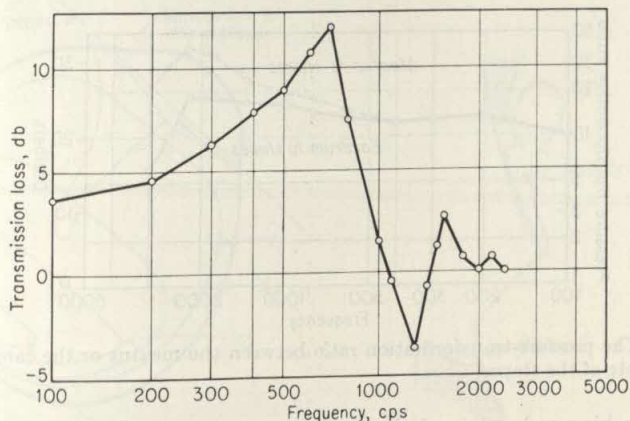


FIG. 5-3. The effects of static pressure on transmission through the middle ear.

auditory ossicles shifted out of their normal direction of vibration and the stapes began to rotate along its longitudinal axis (see page 112 and Stuhlman).

It is of interest that these abnormal modes of vibration, together with a significant reduction in the pressure transformation, occur even for small sound pressures when there is disease of the middle ear. Only this sort of stapelial vibration could be found in a temporal bone that was probably diseased because the opposite ear was filled with pus. It is possible that many spontaneous improvements of acuity in the presence of middle-ear disease can be attributed to changes in the direction of vibration.

It was further established that the pressure transformation is at a maximum in a temporal bone that is fresh and quickly prepared. Every change thereafter leads to a decrease. If, for example, during the sound-pressure measurements the eardrum was exposed to a steady positive or negative pressure of 10 cm of water, there was a noticeable impairment of transmission for tones up to about 800 cps, as shown in Fig. 5-3. Beyond

1000 cps this effect was small. Changes of loudness as observed by normal subjects for steady positive and negative pressures gave the same absolute values and the same relations to frequency (*cf.* page 360). These changes of loudness cannot be accounted for, as they usually have been, by supposing that the steady pressure pushes the stapedial footplate into the oval window. In the measurements of pressure transformation the stapedial movements were fully canceled so that the stapes remained motionless, and thus its manner of attachment to the walls of the middle ear could not have any significance. It is much more likely that the eardrum in its normal condition moves like a piston, because of its conical form, and transmits the whole alternating pressure exerted on its surface to the auditory ossicles. When a strong air pressure is applied to it, however, it is changed to a stretched membrane and transmits much less pressure to the ossicles, as already mentioned.

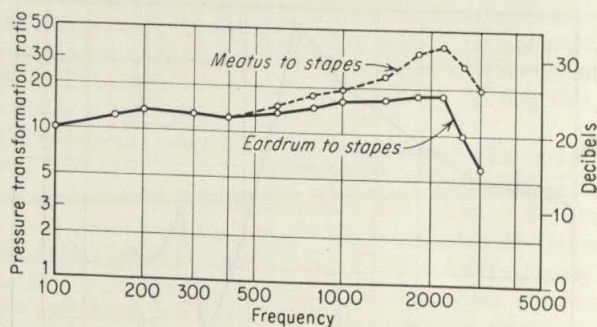


FIG. 5-4. The pressure-transformation ratio between the meatus or the eardrum and the footplate of the stapes.

A disturbing reduction of the pressure transformation, apparently due also to a stretching of the eardrum, arose from a slow drying of the temporal bone. It was found desirable to carry out the preparation of the specimen in a room with a low temperature and a saturated atmosphere. To reduce the drying effect of the mass of plaster in which the bone was held, a lacquer was sometimes used. To prevent an acceleration of the drying by the cement, small woolen threads were placed in the external and internal meatuses to act as wicks to transport water in from the outside.

It is improbable that the tension of the tensor muscle is great enough to change the eardrum from a pistonlike membrane to a stretched membrane. If a weak low tone is listened to with one ear, there will be a decrease in loudness if a bilateral tensor contraction is produced by sounding a shrill tone in the opposite ear.

In Fig. 5-4 is shown the relation between the sound pressure acting on the stapedial footplate and the sound pressure acting on the eardrum, when the stapes is completely motionless. These measurements were made in a temporal bone that was specially selected and rapidly prepared. The broken curve represents the pressure transformation as measured at

the entrance of the external meatus. The solid curve represents the condition when the pressure was measured immediately in front of the eardrum. Though the frequency relations were similar in nearly all specimens, there were many temporal bones in which, despite all precautions, the pressure transformation was one-third to one-fourth of this amount. It seems likely that prolonged disease conditions before death had produced changes in the middle ear.

The frequency function for the pressure transformation between eardrum and stapes shows that up to 2400 cps the eardrum communicates its pressure to the manubrium independently of the frequency. It follows that the natural frequency of the eardrum is relatively high.

Form of Vibration of the Eardrum. Direct measurements of the vibrations of the eardrum by means of a capacitive probe indicated

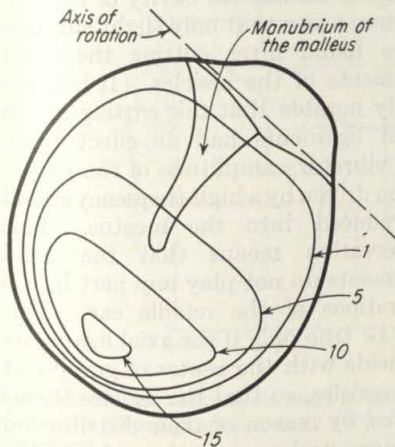


FIG. 5-5. Equal-amplitude curves for eardrum vibrations at frequencies below 2000 cps.

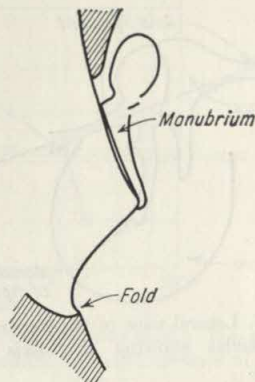


FIG. 5-6. Cross-sectional view of the eardrum.

that the whole eardrum vibrates as a stiff surface along with the manubrium, as seen in the equal-amplitude curves of Fig. 5-5. In this motion the surface rotates about an axis at one edge. Because of this rotation the vibratory amplitude is greatest at the edge below the manubrium. The conical form of the eardrum acts so as to ensure a close coupling between eardrum and manubrium. At the same time it is necessary, just as in a dynamic loudspeaker diaphragm, that the membrane be easily movable at its edges. In fact it is found, as Fig. 5-6 shows, that at the lower edge, in the region where the movement is greatest, there is a prominent rounded fold with a radius of curvature of 0.5 to 0.8 mm. The great elasticity of the fold makes it possible for the membrane to be displaced without appreciable deformation. The fold often is not represented in the figures of anatomical handbooks, and in many specimens it is only weakly developed. It is likely that this particular portion of the eardrum loses its compliance as a result of disease

and drying, whereupon the eardrum ceases to act as a stiff piston and its transfer of pressure to the manubrium is reduced.

Measurements showed that an area of about 55 sq mm out of the total area of 85 sq mm of the eardrum is stiffly connected to the manubrium. As the surface of the stapedial footplate is 3.2 sq mm and the lever arm of the ossicles has a ratio of 1.3:1, the pressure transformation has a theoretical value of 22.

Beyond 2400 cps the conical portion of the eardrum loses its stiffness, and the manubrium in its motion lags behind the motion of the adjacent portion of the membrane.

Suspension of the Ossicles. Since in the measurements of pressure transformation the stapes remained at rest, it is clear from the foregoing that the middle portion of the eardrum also was stationary. Moreover, no changes were produced from opening the middle-ear cavity or cutting the tensor-tympani tendon. It is of interest also that only slight changes

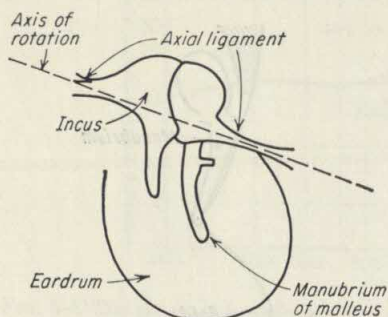


FIG. 5-7. Lateral view of the eardrum and ossicles showing the axis of rotation.

were found after cutting the axial ligaments of the ossicles. It is especially notable that this cutting of the axial ligaments had no effect upon the vibratory amplitude of the stapes when driven by a high-frequency sound introduced into the meatus. This observation means that the axial ligaments do not play any part in the vibrations of the middle ear. This can be true only if the axial ligaments coincide with the center of gravity of the ossicles, so that the ossicles themselves, by reason of their distribution of mass, undergo rotations about this axis. In this manner nature has succeeded in establishing the rotational axis of the ossicles for the high frequencies in a precise way without any need for stiff ligaments. This explains the remarkable paradox that at high frequencies the ossicles vibrate in a precise way even though the whole system lies relatively free in the middle ear. The advantage of this arrangement is that no tensions are set up in the system through variations of friction in the suspension.

In Fig. 5-7 it is apparent that what seems at first to be a superfluous mass of malleus head and incus is really necessary in order to make the center of gravity of the ossicles coincide with the axis of rotation of the ligament. E. Bárány (1) has already shown that this symmetrical distribution of mass about the axis of rotation is true for all mammals and operates particularly in the protection of the ear against vocal sounds transmitted by bone conduction.

If the sound pressure at the external meatus is kept constant, there is a change for tones below 200 cps after the axial ligament is cut. The pressure transmission is unstable and varies according to the position of the temporal bone. This indicates that for the low frequencies, for which

the mass effects are small, the axis of rotation is determined by the ligaments. It is likely, therefore, that the decrease of transmission often observed below 200 cps, as seen in Fig. 5-4, is due to a lack of stiffness of the ligamentous structure.

Frictional Forces in the Middle-ear Mechanism. As the capacitive probe can easily be calibrated by means of an electrodynamic vibrator system, an attempt was made to measure the amplitudes of vibration of the stapedial footplate for constant sound pressures on the eardrum at various frequencies. The method is described in detail on page 97. For this purpose the amplitude of the carrier signal was kept constant, and the end of the probe was shifted along the footplate parallel to its surface until a maximal sound intensity was obtained, as indicated by the loudspeaker connected to the probe amplifier. Because the footplate in

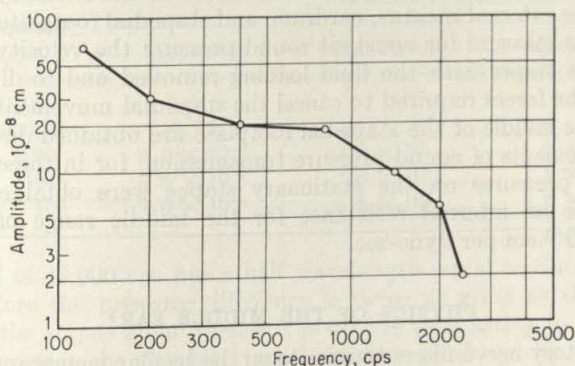


FIG. 5-8. The transformation ratio in the absence of the cochlear fluid. The abscissa shows the stapedial amplitude in 10^{-8} cm for a constant eardrum pressure of 1 dyne per sq cm.

its vibration rotates about an axis at one edge, this procedure gave a measurement of the vibratory amplitude at a point farthest away from the axis of rotation. Figure 5-8 shows for various frequencies the mean values of vibratory amplitude observed in fresh preparations when the eardrum was stimulated by sound pressures of 1 dyne per sq cm. Though these measurements showed considerable variability and were particularly dependent on the conditions of humidity prevailing during the preparation and the measurements, it is clear that the stapedial movements are related to frequency, and up to 2000 cps they fall off approximately in proportion to the frequency.

The edges of the stapes are held in the oval window by a narrow membrane, which limits the movement to little more than 0.1 mm. Therefore it has been assumed up till now that the stapes is maintained in the window by strong elastic forces, and that its displacements are in opposition to these forces. The decline of stapedial movements with the rise in frequency, however, suggests that for the middle range of tones the movement of the ossicles is determined principally by frictional forces.

The middle ear, it seems, acts as a movable piston with great friction. The friction is partly due to the dragging action of the middle-ear muscles.

It appears further that the ossicular system, loaded with the cochlear fluid, constitutes a strongly damped vibratory mechanism with a natural frequency around 1400 cps.

Unfortunately the measurements of impedance at the eardrum do not provide data on the movements of the manubrium, for the upper portion of the eardrum contains a yielding membrane (the pars flaccida) whose characteristics are included in the impedance measurements.

According to Thévenin's theorem, a complex vibratory system can always be replaced by a single vibratory element with a particular internal resistance (Firestone, 2). A calculation can then be made of the vibratory relations in an external system by the use of this internal resistance.

In order to determine the internal resistance of the whole system consisting of the external meatus, eardrum, and stapedial footplate, it is only necessary to measure for constant sound pressure the velocity of movement of the stapes with the fluid loading removed and to divide these values by the forces required to cancel the stapedial movements. These forces at the middle of the stapedial footplate are obtained directly from the measurements of sound-pressure transmission, for in these measurements the pressures on the stationary stapes were obtained. These results gave an internal resistance for the middle range of tones of $R = 1 \times 10^{-3}$ cm per dyne-sec.

PHYSICS OF THE MIDDLE EAR*

The auditory nerve fibers terminate on the basilar membrane, and it is through the vibrations of this membrane that auditory sensations arise.

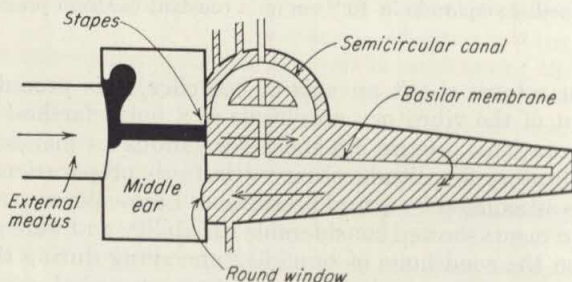


FIG. 5-9. Schematic representation of the cochlea.

Figure 5-9 shows in a schematic way how sound pressure entering the external meatus passes through the eardrum, ossicles, and stapes so as to act only on one side of the basilar membrane. The pressure is relieved by way of the round window. The aerial vibrations of the middle ear are prevented from acting directly on this window. Under these conditions a particular sound pressure produces a maximum movement of the basilar membrane.

* Article 25 as listed in the Author's Bibliography. Published in 1936.

Complete Absence of the Eardrum. If the eardrum is absent the sound pressure is able to reach the stapes and round window at the same time without hindrance, so that only the difference of pressure in these two pathways affects the basilar membrane. If the sound passes freely in the direction of the line connecting the stapes and round window and suffers no reduction in so doing, then the pressure difference is $D = 2a \sin \pi nd/c$, when a is the amplitude of sound pressure, n the frequency, c the velocity of sound, and d the distance between stapes and round window. The distance from the center of the stapedial footplate to the middle of the round window rarely exceeds $d = 0.4$ cm, so that the pressure difference takes values for different frequencies as shown in Table 5-1.

TABLE 5-1

Frequency, cps	$\sin \pi nd/c$	Relation to normal threshold	
		Calculated	Measured
43,000	1		
10,000	0.35		
1000	3.6×10^{-2}	2.8×10	1.6×10^3
100	3.6×10^{-3}	2.8×10^2	1.1×10^2
10	3.6×10^{-4}	2.8×10^3	0.9×10

A sound of 43,000 cps has a half wavelength equal to the distance d , and therefore the pressure difference is twice as great as the pressure acting on the stapes alone (hence it is double that acting in the normal ear if we neglect the pressure transformation produced by the ossicles through their lever ratio). We can assume therefore that the pressure differences shown in the table (at least below 1000 cps, where resonances in the middle ear need not be considered) indicate the degree to which the action on the basilar membrane is reduced when the eardrum is absent. Actually the pressure difference is even smaller than this because the sound is not freely transmitted through the middle-ear cavity. Especially is this true at low frequencies for which the phase differences between the two windows become much smaller. Therefore, as the second column of the table shows, the tones up to 1000 cps suffer a raising of the threshold that is proportional to the frequency.

To determine whether hearing without the eardrum is the result of a pressure difference between the stapes and round window or whether it is due to something else, the threshold was measured on five persons with a unilateral loss of eardrum, malleus, and incus and after an otological examination had shown that the inner ear was normal. In Fig. 5-10 the short-dashed curve shows the mean values obtained for the normal ear, and the solid curve shows the means for the impaired ears. The long-dashed curve shows normal thresholds obtained in another study (page 258). Here the ordinate represents the sound pressure at the eardrum or in the middle ear. It is especially to be noted that for the high tones the acoustical impedance of the auditory meatus can be greatly altered when

the eardrum is absent, so that erroneous results will often be obtained if the threshold is measured with an earphone without measurements of the impedance of the meatus at the same time. It must also be borne in mind that the noisiness of the room in which the measurements are made affects the two thresholds unequally.

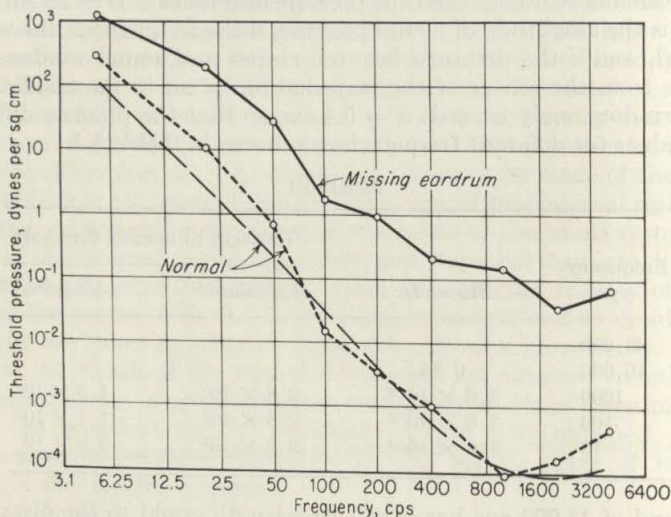


FIG. 5-10. Thresholds for normal and impaired ears.

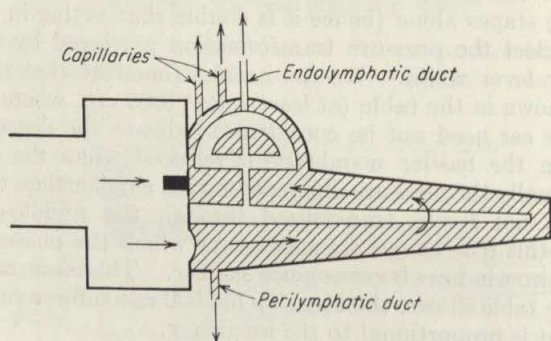


FIG. 5-11. Fluid pathways in ears without drum membranes.

Figure 5-10 (as well as the last column of the table) shows that the impairment of sensitivity becomes greater as the frequency rises. Therefore something apart from the pressure difference between stapes and round window must be considered as producing the effects.

Anatomically it seems probable that when pressure is exerted on both windows at the same time the walls of the inner ear will not be completely unyielding, but that streaming of the fluid will be permitted by the various blood vessels. Figure 5-11 shows schematically the paths that the fluid may take outside the inner ear.

If we compare the possibilities for fluid flow on both sides of the basilar membrane and consider the number of capillaries and their lengths in the firm bony wall, it seems likely that the flow will be much easier on the stapes side than on the round-window side. (The vessels of the cochlea, which are not shown in the figure, are fully symmetrical on the two sides.) Therefore, if the same pressure acts on both windows, there will be a flow of fluid and a displacement of the basilar membrane which is just opposite in direction to that produced when the eardrum is present. Hence there is simply a phase reversal of the fluid motion in the cochlea without any change of form, because most of the paths permitting the flow of fluid are at the basal end of the cochlea. It follows that in this sort of hearing the tonal sensations are unaffected except for being reversed in phase.

For constant pressure a sinusoidal oscillation of fluid in a capillary decreases as the frequency rises. Therefore it is to be expected that when

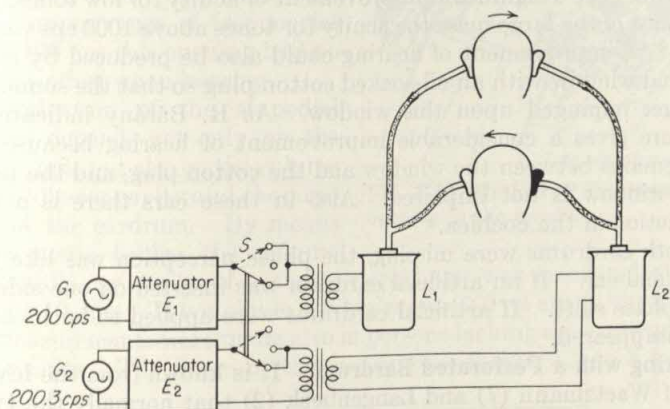


FIG. 5-12. Arrangement for measuring phase reversal in an ear without a drum membrane.

the eardrum is missing the sensitivity will become poorer as the frequency increases, as the measurements have indicated.

The phase reversal can be demonstrated in the perception of the direction of sounds. For this purpose it is convenient to employ rotating tones of about 200 cps. The arrangement is shown in Fig. 5-12.

By means of attenuators E_1 and E_2 the loudness of two tones of 200 and 200.3 cps was adjusted for equality, with the switch S operated so as to present the tones alternately to the two ears of the subject with one eardrum missing (shown in the lower sketch with the defective ear indicated as black). The other observer, both of whose ears were normal, also made an adjustment of equality by clamping the tubes running to his ears. When this was done, the switch S was placed in its lower position so that both tones were heard simultaneously. The subjects perceived a single tone that shifted back and forth inside the head from one ear to the other in accordance with the phase relation (*cf.* Hornbostel, 1). When the position of the tone at any moment was indicated by

pointing with the finger, it became clear that the two observers showed a phase difference of 180° . If two observers whose ears were normal on both sides were used, their pointing showed phase agreement. The success of the experiment depended upon careful equating of the loudness on the two sides, and on the use of tones that were completely free of overtones. The adjustment for equality of loudness was made easier if separate loudspeakers and attenuators were used for each ear, though in this case it was necessary to give attention to the polarity in connecting the speakers.

After the phase shift in the defective ear had been established, this ear was fitted with an artificial eardrum. Thereupon the shift disappeared and the ear behaved normally. If the edges of the eardrum were still present, it was possible to insert a wad of cotton soaked in paraffin oil so that it closed the opening and made contact with the stapes. This sort of eardrum gave a significant improvement of acuity for low tones, though on account of the large mass the acuity for tones above 1000 cps was made worse. An improvement of hearing could also be produced by covering the round window with an oil-soaked cotton plug so that the sound waves no longer impinged upon this window. As R. Bárány indicated, this procedure gives a considerable improvement of hearing because an air layer remains between the window and the cotton plug, and the mobility of the window is not impaired. Also in these ears there is a normal fluid motion in the cochlea.

If both eardrums were missing, the phase perception was like that of the normal ear. If an artificial eardrum was inserted on one side, there was a phase shift. If artificial eardrums were applied to both ears, this shift disappeared.

Hearing with a Perforated Eardrum. It is known from the investigations of Waetzmänn (7) and Langenbeck (2) that normally the two ears of an individual are alike in their threshold sensitivity over the frequency range. Therefore it is possible to evaluate the effects on transmission of a mechanical injury in one ear by comparing the thresholds obtained in the two ears.

Such measurements showed that a lens-shaped tear of the membrane, extending from the end of the manubrium to one edge and having a width of 2 mm, had no noticeable effect on thresholds from 50 to 4000 cps except to alter slightly the small deviation in the frequency function. Below 50 cps there was a slight impairment, which reached about 15 db at 5 cps.

In order to study these unexpected phenomena more thoroughly, a small mirror was applied to the malleus of a fresh cadaver ear by working through the external meatus, much as was done by Köhler (1) on a living subject. It was hoped that by reflecting a light beam from this mirror the changes of vibratory amplitude of the ossicles as a result of a perforation could be determined. Unfortunately it was found difficult to place a mirror of 0.5 sq mm (which was suitable for optical recording) in this position and to determine its angle of inclination.

Therefore, as Fig. 5-13 shows, the meatus was drilled through from below close to the eardrum, in the manner described on page 30, so that

the mirror could be cemented to the manubrium. The edges of the drill hole were covered with thick petroleum jelly to fill all openings in the bone, and a metal ring carrying a glass plate was sealed in the opening. The sound was introduced into the meatus by means of a small olive as usual.

In a completely fresh preparation the vibratory amplitudes of the manubrium were measured as a function of frequency, with sound pressure in the meatus kept constant. Then a hole of 1 sq mm was made in the inferior portion of the eardrum and the measurements repeated. The results over the frequency range are shown in Fig. 5-14. It is plain that over the upper range of frequencies down to 100 cps this opening had no significant effect upon hearing.

The reduction of the stapedial vibrations depends not only on the size of the hole but also on the volume of the middle-ear cavity and the compliance of the eardrum. By means of an acoustic bridge the volume of the middle-ear cavity of a cadaver specimen was measured at a frequency of 10 cps. This volume for males was 2.0 cu cm on the average. These measurements were made also in persons lacking one eardrum, with similar results. The range of the measurements was 1.2 to 3.5 cu cm.

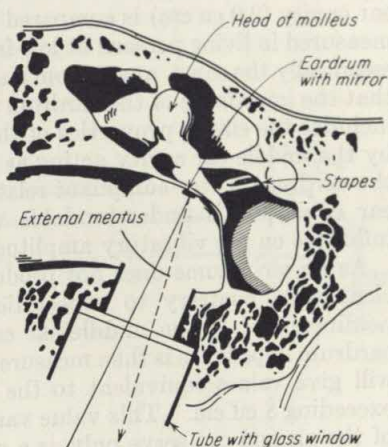


FIG. 5-13. Method of making a lateral opening in the meatus.

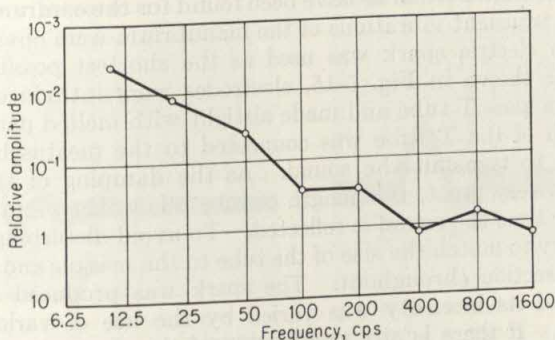


FIG. 5-14. The effect of an eardrum perforation on the amplitude of vibration of the ossicles. The amplitude is shown relative to that observed before the perforation, with sound pressure kept constant.

The portion of the middle ear occupied by the ossicles had a volume of 0.5 to 0.8 cu cm. The further enlargement of the volume occurs because this part of the ear connects with air cells in the surrounding bony wall, especially in the so-called mastoid process. These air cells, shown

schematically in Fig. 5-13, vary greatly in size in different persons and often are so small that it would be proper to say that a portion of the middle-ear cavity is lined with a sound-absorbent material. In any event, this structure reduces the resonance of the cavity.

If the acoustic impedance of an air volume equal to that of the middle-ear cavity (2.0 cu cm) is compared with the impedance of the eardrum as measured in living persons at low frequencies, it is found that the two are essentially the same, apart from a small phase angle (Sivian). It follows that the impedance of the eardrum as measured from the meatus not only includes the elastic properties of the membrane but is greatly influenced by the middle-ear cavity acting as an air cushion. As the membrane of the eardrum is very compliant relative to the elastic forces of the middle-ear cavity, it is understandable why a perforation has such a small influence on the vibratory amplitude.

As an air volume does not produce any nonlinear distortion it is also clear why, contrary to expectations, the middle ear has such slight nonlinearity. If the middle-ear cavity is opened with a drill and the eardrum impedance is then measured, a fresh, well-humidified preparation will give values equivalent to the impedance of an air volume usually exceeding 8 cu cm. This value varies greatly according to the humidity of the air and can serve only as a general indication.

It is to be hoped that it will be possible sometime to introduce a catheter into the middle ear by way of the Eustachian tube and by this means to make a measurement of the true value of the impedance of the eardrum of the living person.

Transient Vibrations of the Eardrum. For an understanding of the form of vibration of the ossicles it is important to know whether, in the course of time, the ligaments in the cadaver specimen undergo the same deteriorations from normal as have been found for the eardrum. For this purpose the transient vibrations of the manubrium were observed. The sound of an electric spark was used as the shortest possible pressure impulse. As shown in Fig. 5-15, electrodes were introduced into two branches of a glass T tube and made airtight with melted paraffin. The third branch of the T tube was connected to the meatus by a tube 2 meters long to transmit the sound. As the damping of the ossicular vibrations is very great, this length of tube allows the vibrations to die down by the time the sound is reflected. To avoid disturbing reflections it is necessary to match the size of the tube to the meatus and to keep the same cross section throughout. The spark was produced by a static machine, and its intensity was varied by the use of various sizes of Leyden jars. If there is any scintillation of the electrodes the pressure pulse will be mixed with noise. This is usually due to humidity and is avoided by a general heating of the T tube. It is further desirable to connect to the T tube a narrow capillary *C*, which prevents a variation of static pressure in the tubes during the heating and thus protects the eardrum.

The meatus was provided with a lateral window, as described earlier, through which a mirror with an area of less than 0.5 sq mm could be

applied for oscillographic observation of the vibrations of the manubrium and eardrum.

The left-hand portion of Fig. 5-16 shows the transient vibrations of the lower part of the eardrum, and the right-hand portion of this figure shows the vibrations of the manubrium. Repeated observations indicated that

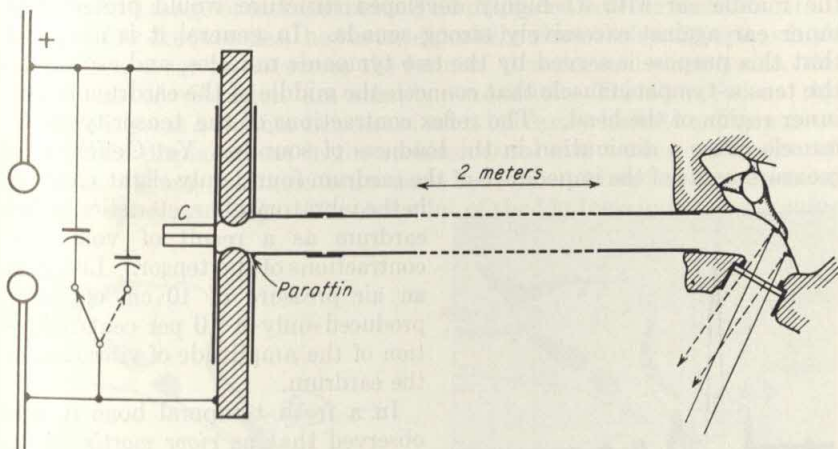


FIG. 5-15. Arrangement for applying a pulse to the eardrum.

the natural frequency of the middle ear was between 800 and 1500 cps, as obtained by Frank and as observed on living persons (page 315). There are hardly noticeable changes in the course of time under proper conditions of humidity. As expected from the fact that the eardrum is only 0.1 mm thick, it dries out much more rapidly than the ligaments.

Inferior portion of the eardrum

Manubrium of the malleus

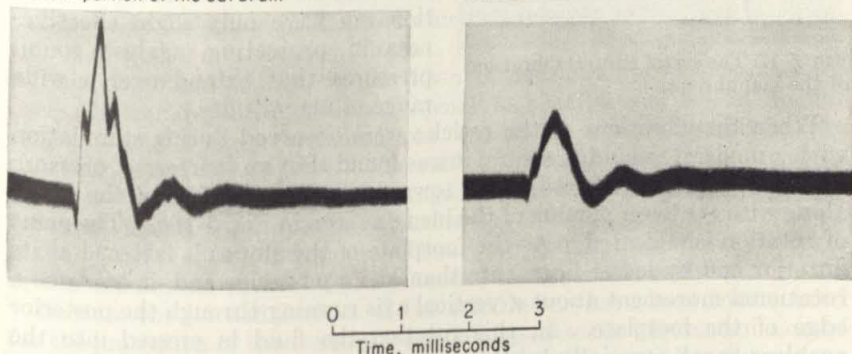


FIG. 5-16. Transient vibrations of the eardrum and the manubrium of the malleus.

The two curves show that strong overtones arose in the eardrum, though these were somewhat reduced at the manubrium. If some cotton was introduced into the tube leading to the ear the sharp onset of the pulse was reduced somewhat, and the overtones were no longer elicited. In this way, as Fig. 5-17 shows, transients were observed that were exactly

like those obtained in the living ear by a clicking of the Eustachian tube. However, the first half-wave is still not to be regarded as a completely free vibration.

Protection of the Middle Ear against Excessive Sounds. Just as the eye is protected against blinding light by the iris, we would expect that the middle ear with its highly developed structure would protect the inner ear against excessively strong sounds. In general it is assumed that this purpose is served by the two tympanic muscles, and especially the tensor-tympani muscle that connects the middle of the eardrum to the inner region of the head. The reflex contractions of the tensor-tympani muscle cause a diminution in the loudness of sounds. Yet Geffcken in measurements of the impedance of the eardrum found only slight changes

in the vibratory characteristics of the eardrum as a result of voluntary contractions of the tensor. Likewise an air pressure of 10 cm of water produced only a 10 per cent reduction of the amplitude of vibration of the eardrum.

In a fresh temporal bone it was observed that as *rigor mortis* set in, in which all the muscles became strongly contracted, the vibratory amplitude of the eardrum and ossicles in response to a constant sound pressure was reduced at most to only a third, though to be sure only a single observation was possible. Therefore it seems that the tensor contraction can have only slight effectiveness in protecting against sound pressures that extend over a wide range of magnitudes.

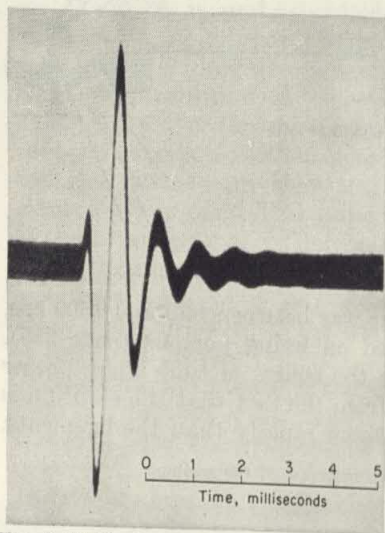


FIG. 5-17. The lowest natural vibrations of the manubrium.

When the vibrations of the ossicles were observed during stimulation with a moderate sound pressure, it was found that an increase of pressure caused the manubrium to move toward the inner region of the head, along with the lower portion of the incus, as seen in Fig. 5-18a. The point of rotation is indicated. As the footplate of the stapes is fastened at its anterior end by looser ligaments than at its posterior end, it executes a rotational movement about a vertical axis running through the posterior edge of the footplate. In this rotation the fluid is pressed into the cochlear canal, especially by the anterior portion of the footplate.

If the amplitude of motion of the eardrum was made still greater, this form of vibration finally came to a sudden end and consistently went over into another form in which the stapes rotated about an axis running longitudinally through the footplate. Then the fluid of the inner ear merely shifts from the upper half of the footplate to the lower, without causing any displacement in the cochlear canal. As the footplate of the

stapes is rather small, this is a means of limiting the transmission of an excessive vibration of the eardrum to the fluid of the inner ear.

For frequencies above 100 cps the transition from one form of vibration to the other takes place in such a way that for large sound pressures the two are superimposed, and for further increases of sound pressure there is an extensive range of increase in the fluid displaced into the cochlear canal. For the low frequencies, however, especially those below 20 cps, which most often occur in nature in the form of thunder and windstorms, the two forms of vibration are sharply separated. Therefore, when the pressure is great a further increase of sound pressure leads to a diminution in the fluid displacement in the cochlear canal and hence a reduction of loudness. These loudness reductions have been observed for tones of 5 and 10 cps (page 263). The end point of the loudness increase coincides

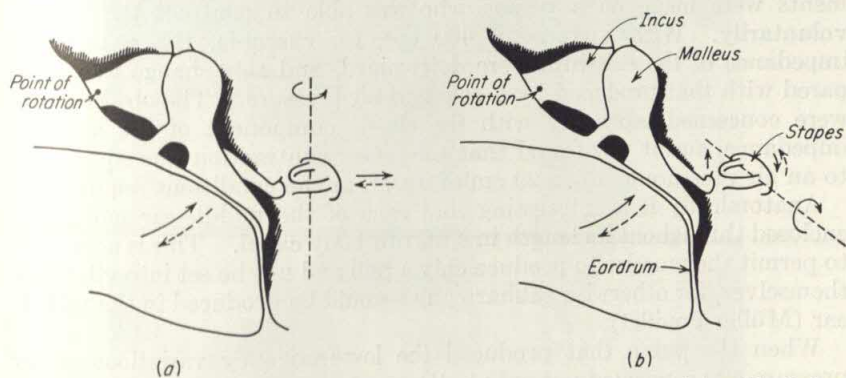


FIG. 5-18. Forms of vibration of the ossicles; (a) shows the form at intensities below the threshold of feeling and (b) the form at intensities above this threshold.

exactly with the sound pressure at which the change of the form of vibration is observed in a fresh specimen.

This important change in the form of vibration of the ossicles for excessive sound pressures is made possible because the ossicles do not vibrate about a fixed rotational axis, but about a point formed by the short process of the incus and the wall of the middle ear. The freedom of the ossicular vibrations is increased by reason of the fact that the vibratory axis of the stapes is inclined about 20 to 35° from the vibratory plane of the malleus and incus. Thus we begin to understand the form of the middle ear, which otherwise seems unnecessarily complex.

Because the jointed ossicles of the middle ear have been constructed for the protection of the inner ear, a difficulty arises in the transmission of vibration from one ossicle to the next. A distortion could easily appear at the joint. If the contact pressure between two vibrating bodies is smaller than the accelerating force acting during the vibration, the two bodies will separate and the result is like the well-known phenomenon of the bouncing sand grains on a vibrating plate (Andrejew; Strutt, 7). If the vibrations are small, the elastic ligaments are able to exert a pressure that is sufficiently great that no special measures are necessary. For

larger vibrations, however, this is no longer true and it becomes clear why muscles are present in the middle ear that work opposite to one another and press the stapes against the incus while, at the same time, the other ligaments are stretched.

The accelerating forces for sinusoidal vibrations are proportional to the amplitude and to the square of the frequency, and hence it is to be expected that these two muscles will respond especially for the high tones and contract more vigorously as the sound pressure increases, as actually is the case.

The maximum acceleration forces in the middle ear for which no distortion should occur are given by the pain and tickle thresholds and are of the order of 20 grams (19,600 dynes per sq cm). To test whether the tensor-tympani muscle can produce a force of this magnitude, measurements were made on a person who was able to contract the muscle voluntarily. With a tone of 400 cps, for example, the changes of impedance of the eardrum were determined, and this change was compared with that produced by a constant air pressure. The observations were concerned especially with the elastic component of the acoustic impedance, and it was found that the tensor contraction was equivalent to an air pressure of 10 to 20 cm of water, as the conditions require.

Anatomically it is interesting that each of the middle-ear muscles is enclosed throughout its length in a narrow bony canal. This is necessary to permit the muscles to produce only a pull and not be set into vibration themselves, for otherwise subharmonics would be produced in the middle ear (Müller-Pouillet).

When the pump that produced the low-frequency variations of air pressure was connected not only to the meatus of the specimen but also to a manometer and to the meatus of a subject, it was observed that the appearance of the second form of vibration in the cadaver corresponded to the arousal of sensations of pain in the living ear.

In the frequency region of 0.5 to 10 cps almost all subjects report that the pain threshold arises through contact or friction between two surfaces in the middle ear. Especially for long-continued action of pressure there is an impression that some particular small surface has become chafed. It is possible that in the changing of the forms of vibration the ligaments and joints of the ossicles are excessively stretched and pain is thereby elicited. It is even more likely, however, that in the rotation of the stapes about its longitudinal axis the two crura come in contact with the lateral walls of the middle ear, because the stapes, as Fig. 5-19 shows, lies deep in a narrow niche. This figure shows the two crura of the stapes and the right and left side walls of the niche. The actual distance between the crura and the right wall is even smaller than indicated, for in this specimen the mucous membrane on the bone was intentionally dried out in order to make the two crura more visible. The same relations are seen in a microscopic section prepared by Keith (see Wrightson).

It may be assumed that the limited width of the niche provides a limit to the lateral amplitude of vibration of the stapes, for the observations showed that despite strong amplification of the vibrations of the eardrum the lateral movement of the stapes remained constant and the vibrations

were dissipated in the ligaments of the malleus and incus. This condition provides further insurance against excessive vibrations. However, a movement in the joint between malleus and incus could not usually be observed (*cf.* Helmholtz, 2); this joint is apparently ankylosed.

The stapes is close to the wall, especially on the right side, so that once every vibration a contact is made. It could be shown with a manometer

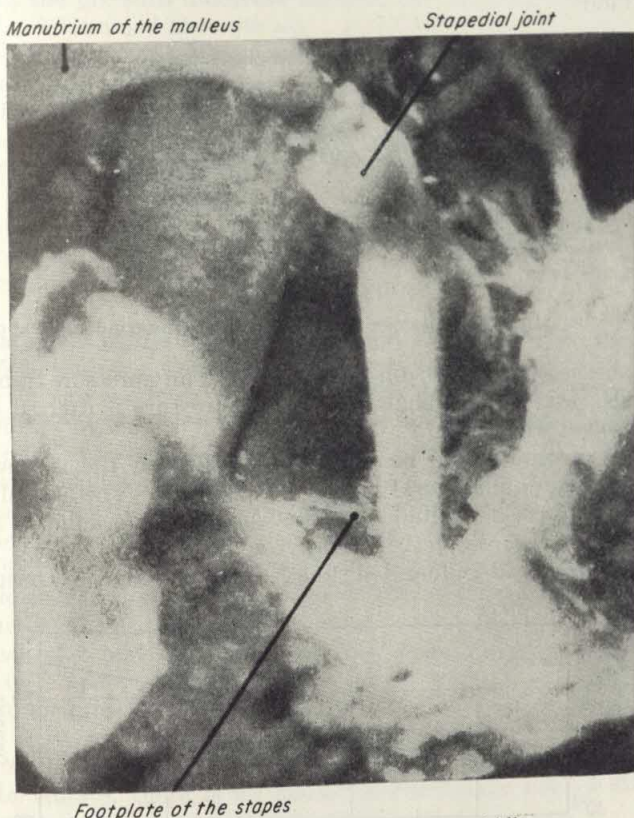


FIG. 5-19. Position of the stapes in the middle ear.

that for a sound of 1 cps a break appeared during every cycle at the pressure maximum, in full agreement with the anatomical observations.

The sensations of contact are to be distinguished from the pain sensations. They provide a general feeling of pressure over the whole surface of the meatus, the eardrum, and the middle ear.

DIFFERENCES IN SOUND PRESSURE BETWEEN THE COCHLEAR WINDOWS*

In the normal ear the vibrations of the eardrum are transferred by the ossicles to the oval window. As indicated above (page 100), the mecha-

* Article 48 as listed in the Author's Bibliography. Published in 1947.

nism of the middle ear is such that the pressure amplitude on the footplate of the stapes is about twenty times greater than the pressure amplitude at the eardrum. The magnitude of this pressure transformation is independent of frequency up to about 2400 cps. Because the pressure on the footplate of the stapes is much greater than at the eardrum or in the middle ear, it is this pressure that determines the vibration of the cochlear fluid.

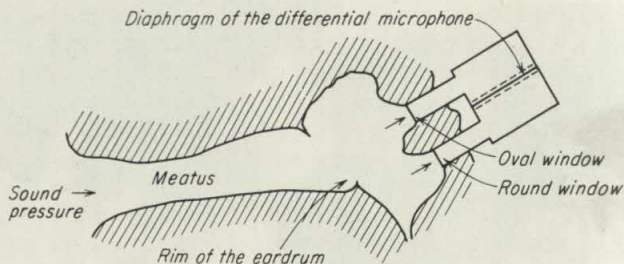


Fig. 5-20. Schematic representation of the ear without the conductive apparatus.

In the absence of the eardrum there will not be any pressure transformation. Then, as Fig. 5-20 shows, the sound pressure is exerted on both oval and round windows.

A static pressure would be impressed equally on the two windows, according to the fundamental law of hydrostatics. There would be no displacement of cochlear fluid from one window to the other. A sound pressure, however, may act differently on the two windows. Because these windows are at different distances from the auditory meatus the

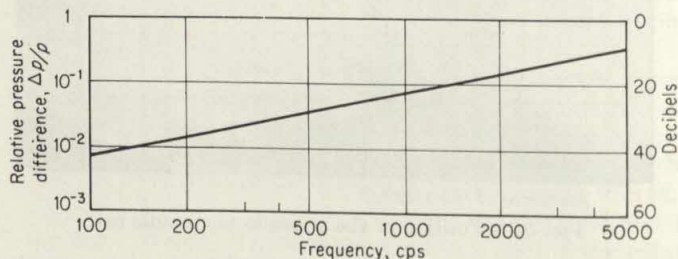


Fig. 5-21. The pressure differences Δp existing in a progressive wave at points 4 mm apart, expressed in relation to the pressure p at one point.

sound may not reach them at the same time. Because the distance between the two windows is small, the pressure difference is small also. To estimate its magnitude we can consider the sound field in a tube at two points separated by 4 mm along the longitudinal axis. This distance corresponds to the distance between the centers of the two windows. Figure 5-21 shows, for various frequencies, the relation between Δp , the pressure difference between the two points, and p , the pressure at one of them. At 100 cps, for example, Δp is less than 1 per cent of p , and

so if this condition held for the ear the applied sound would be very ineffective.

Actually, the middle-ear cavity forms a resonance chamber, and it is to be expected that the pressure difference between two points within this chamber will be even smaller than along a tube. Because of the irregular form of the cavity and the many niches in which the sound can be absorbed, the pressure difference between the oval and round windows cannot be determined theoretically. In previous literature it was often concluded on geometrical grounds that the sound pressure was smaller at the round window than at the oval window because the round window lies in a niche. However, as the wavelength of a sound is large compared with the dimensions of the niche, this conclusion is invalid.

Sometimes when the eardrum is missing the person suffers a much smaller impairment of hearing than would be expected on theoretical grounds. Therefore it is necessary to measure the actual pressure differences that occur at various frequencies. Such measurements are of particular interest in middle-ear cavities that have been enlarged by surgery.

Measurement of the Pressure Difference by the Reciprocity Method.

As Fig. 5-20 shows, it would be possible to measure the pressure difference between the two windows with a differential microphone connected to the two windows by two small tubes. However, the pressure difference is small in relation to the whole pressure, and such a differential microphone would have to fulfill exceedingly severe conditions of symmetry and would be difficult if not impossible to construct. Also, the microphone capsule adds a new cavity to the middle ear. Unless this cavity is small relative to the middle-ear cavity, *i.e.*, has a volume of only a few cubic millimeters, the whole distribution of sound pressure in the middle ear will be altered. It does not seem feasible to produce differential microphones of sufficiently high sensitivity and impedance, and for this reason it has not been possible in the past to make such measurements.

These difficulties can be overcome, however, by employing Helmholtz's principle of reciprocity (see Rayleigh). According to this principle, if a microphone is acted upon by a sound source by way of some system that is able to vibrate, there is no change in the acting force if the sound source and microphone are interchanged.

In order to measure the difference in sound pressure between the two windows of the cadaver preparation shown in Fig. 5-20 the two symmetrical microphone capsules were replaced by two identical loudspeakers. Those speakers were made to produce identical sound pressures but in exactly opposite phase. The phase opposition corresponds to the differential effect. If now a condenser microphone was connected with the meatus, it was possible to calculate the pressure difference between the two windows from the intensity recorded by the microphone.

If the paths taken by the sound from the two loudspeakers to the microphone at the entrance of the auditory meatus are exactly the same there will be complete silence at the microphone because the two sounds are equal in amplitude but opposite in phase. The sensitivity of the

system is limited by the sensitivity of the condenser microphone. Since the sensitivity of the human ear is greater than that of any microphone, it is better to replace the microphone with the ear of a subject. However, the ear of a subject is not satisfactory for direct measurements of sound pressure. Therefore the procedure was changed, and the ear was used as a null indicator. The sound pressure in one loudspeaker was adjusted in amplitude and phase until no sound was audible from the meatus of the preparation. The change of amplitude from equality that was required to obtain silence showed directly the difference in amplitude between the two windows, and the necessary change in phase represented the phase difference.

The loudspeakers had to be connected to the windows without any increase in the volume of the middle ear. This was accomplished by

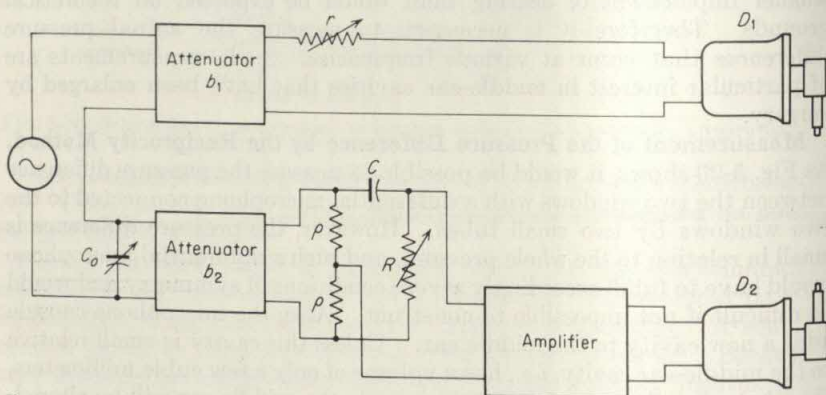


Fig. 5-22. Apparatus for measuring the difference in sound pressure between oval and round windows.

inserting a narrow capillary between window and loudspeaker. Capillaries 10 mm long and of about 0.1 mm inside diameter were used. Through these capillaries the sound pressure was delivered to the middle ear. The energy loss was compensated by increasing the current to the loudspeakers. The frictional resistance of the capillaries prevented any significant change in the effective volume of the middle ear.

The arrangement of the apparatus is shown in Fig. 5-22. An a-c generator supplied the two attenuators b_1 and b_2 , which were connected in series. Attenuator b_1 operated a dynamic-horn type of loudspeaker D_1 connected to one capillary. The other attenuator b_2 was followed by a phase shifter and an amplifier, and operated a second loudspeaker D_2 connected to the other capillary. The phase shifter consisted of two resistances ρ and ρ , a resistance R , and a condenser C . The value of 2ρ was made equal to the impedance of the attenuator. The condenser C was made as small as possible to prevent a shorting of 2ρ through C and R . The amplifier had an extremely high input impedance. The phase of the current through D_2 was changed relative to the current through D_1 by varying the resistance R without any change in the amplitude.

If ω is the angular frequency of the alternating current and dR is the change in resistance of the phase shifter, the phase change $d\alpha$ in radians is

$$d\alpha = \frac{2\omega C}{1 + \omega^2 C^2 R^2} dR \quad (5-1)$$

It is advisable to keep R as small as possible. This can be done by shifting the phase by means of a condenser C_0 . When R is small the above formula is simplified to

$$d\alpha = 2\omega C dR \quad (5-2)$$

Attenuator b_1 must be adjustable to 0.001 db, which is accomplished by a series resistor r as shown. The amplifier must have a large amount of negative feedback to give it sufficient stability for the precision required.

Technique of the Measurements.

To measure the pressure difference between the two windows the two loudspeaker systems were first adjusted to give sounds of the same amplitude but opposite phase. The loudspeaker systems were constructed so as to be as symmetrical as possible and were connected to a small capsule as shown in Fig. 5-23. Attenuator b_1 and resistance R were adjusted until nothing was heard in the rubber tube leading from the capsule. The sound from one loudspeaker was then completely absorbed by the other loudspeaker, and none could enter the ear. The amplitudes of the speakers were then equal but of opposite phase.

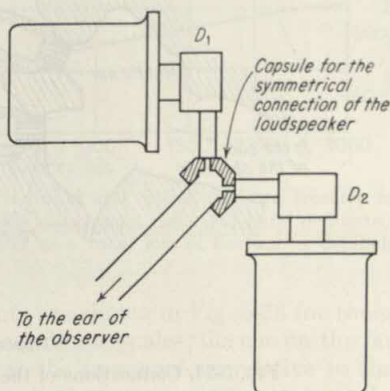


FIG. 5-23. Arrangement for adjusting the two loudspeakers of the preceding figure to the same amplitude and opposite phase.

Now the loudspeakers were connected to the oval and round windows in the manner indicated in Fig. 5-24. In order to place the loudspeakers in an exact manner at the two windows, short pieces of brass tubing were cemented in the windows with dental cement, as shown. The joints were made airtight with petroleum jelly. Listening was done with a tube connected to the meatus of the preparation, and in general a tone was then heard, and a readjustment of attenuator b_1 and resistance R was necessary to restore the null. The change Δb_1 then represents the intensity difference and the change ΔR represents the phase difference in the paths from the windows to the meatus.

Control Experiments. A test of the arrangement described above was carried out by measuring the velocity of propagation of sound along a tube with a constant inside diameter. The propagation of sound along a tubular conduit is well known, so that both its velocity and attenuation

can be calculated. As it is necessary to have a sound field that is free of reflections, a brass tube with an inside diameter of 7 mm and a length of 6 meters was used, with one portion containing thin cotton yarn in increasing amount toward the end, as shown in Fig. 5-25. The yarn served to absorb the sound and thereby to prevent reflection from the end. The

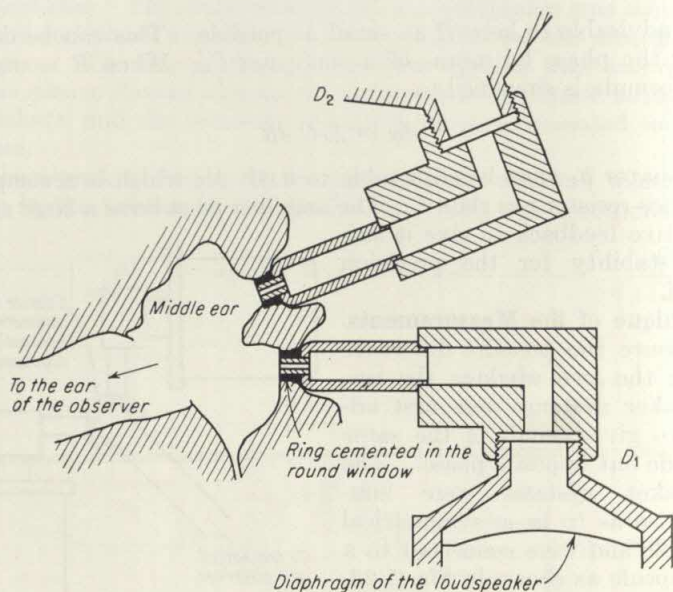


FIG. 5-24. Connections of the loudspeakers to the middle ear.

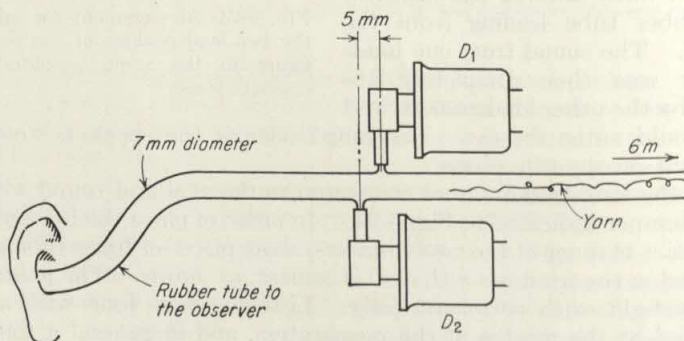


FIG. 5-25. Measurement of sound velocity in a tube by the reciprocity method.

other end of the brass tube was connected to the ear by a rubber tube. Near this end were two small openings 5 mm apart to which the two loudspeaker capillaries could be fitted. The adjustment for a null as described above gave the change of sound velocity and of phase over the distance of 5 mm. These measurements agreed with the calculated values within 5 per cent for tones between 200 and 3000 cps. The

precision was limited by the harmonic content of the sound, and thus by the oscillator and filters available. Closing the far end of the tube had no effect on the adjustment, which proved that there were no disturbing reflections.

Sound-pressure Differences between Oval and Round Windows. For these measurements fresh temporal bones were used in which all openings made during dissection were closed with dental cement. The tube leading from the meatus of the specimen to the ear of the listener was kept as straight as possible, since a departure from the axis of the meatus can cause a phase change.

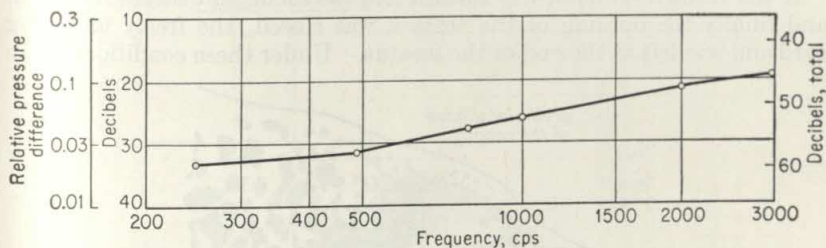


FIG. 5-26. The pressure difference Δp between oval and round windows, relative to the pressure p in the meatus. This relation is shown as a ratio (left-hand ordinate), in decibels (second ordinate on the left), and as a total loss of hearing in decibels (right-hand ordinate).

Results of the pressure measurements are shown in Fig. 5-26 for tones from 250 to 3000 cps. There are three ordinate scales; the one on the far left represents the pressure difference at the two windows relative to the total pressure, and the next one represents the same variation in decibels. However, this scale does not show the complete loss of sensitivity, for when the middle-ear mechanism is intact there is a twentyfold pressure transformation between eardrum and stapes, which gives a gain of 26 db. Therefore if a comparison is made of the pressure difference as measured

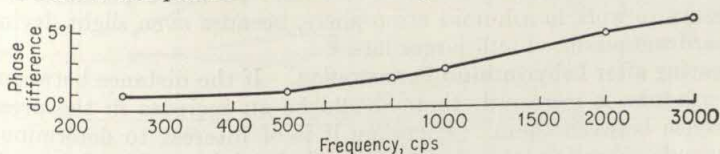


FIG. 5-27. The phase differences between oval and round windows.

and that existing in a normal ear it is necessary to add 26 db to the loss, as shown by the scale on the right. With increasing frequency the pressure difference between the two windows becomes greater, and at 3000 cps it is as much as one-tenth of the sound pressure in the meatus. Phase differences between the two windows are shown in Fig. 5-27.

These results show the hearing loss that should appear after loss of the eardrum if the pressure difference between the two windows is the determining condition. This loss should be about 60 db for tones below 500 cps, and somewhat less for higher tones, approaching 45 db at 3000

cps. However, in clinical practice such great losses are not observed after a simple loss of the middle-ear apparatus. It follows that the determining condition is not the pressure difference between the two windows. In fact, there is evidence that displacements of the cochlear fluids can arise through different mechanisms when the eardrum is lacking (page 105). It is possible also that the mechanism changes with frequency. To decide among the different possibilities, the loss should be calculated for the various possible mechanisms and the one chosen that gives the smallest loss. This mechanism then will determine the threshold of audibility.

If the tegmen tympani was opened and the incus and stapes removed, and finally the opening of the tegmen was closed, the freely vibrating eardrum was left at the end of the meatus. Under these conditions there

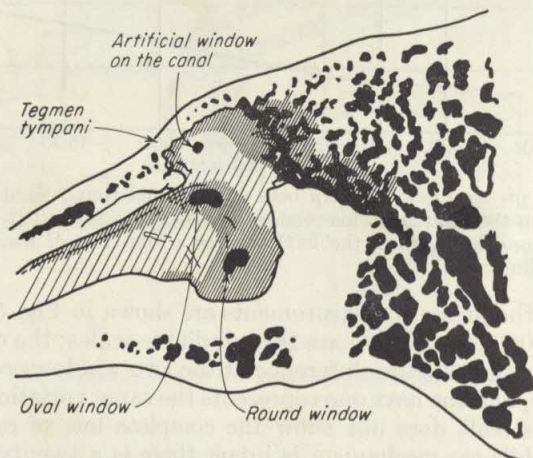


FIG. 5-28. The resonance chambers of the middle ear.

was an additional hearing loss of 1 to 5 db. In this experiment it was necessary to work in a humid atmosphere, because even slight drying of the eardrum produced still larger losses.

Hearing after Labyrinthine Fenestration. If the distance between the two windows is increased, there should be an increase in the pressure difference between them. Therefore it is of interest to determine the magnitude of hearing losses to be expected after labyrinthine fenestration. To that end the oval window was filled with plaster, and an opening was made in the ampulla of the horizontal semicircular canal. The new opening was located on the line connecting the oval and round windows and in such a way that the oval window was halfway between it and the round window, as Fig. 5-28 shows. The distance between the round window and the new one was about 8 mm. Measurements were then made in the same way as before, with results shown in Figs. 5-29 and 5-30.

The ordinate of Fig. 5-29 shows the sound pressure at the artificial window in relation to the sound pressure at the round window for three different temporal bones. There were large differences among ears, and

the dotted curve shows one in which the sound pressure between the windows varied little below 1500 cps. Figure 5-30 shows the same results expressed as the ratio between the pressure difference at the two windows and the pressure in the meatus. Here the dotted curve shows a total

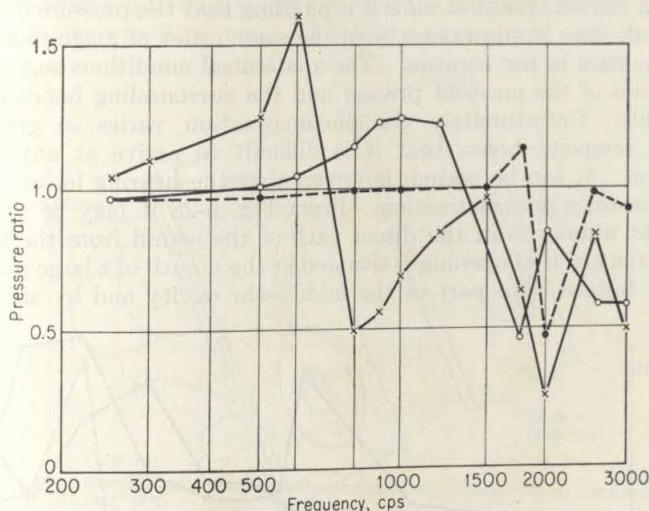


FIG. 5-29. The ratio between the pressure at the artificial window and that at the round window. The three curves represent different ears.

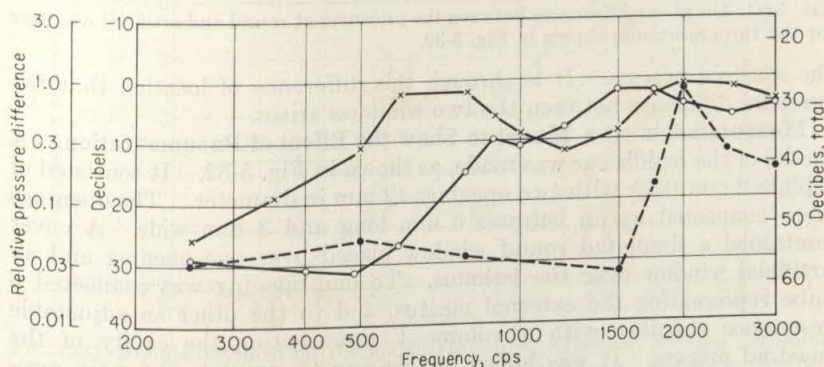


FIG. 5-30. The pressure difference Δp between round and artificial windows in relation to the pressure p in the meatus, shown as a ratio (left-hand ordinate), in decibels (second ordinate), and as a total loss of hearing in decibels (right-hand ordinate). The three curves are for different specimens.

hearing loss around 55 db for tones below 1500 cps. In contrast to this ear, several others showed surprisingly large pressure differences. At times the pressure difference between the two windows reached the order of magnitude of the pressure in the meatus, and then the hearing loss was due mainly to the absence of the pressure transformation by the middle-ear mechanism. In one ear, for example, a total hearing loss of only

30 db was observed in the region of 500 to 3000 cps. Such hearing losses are often observed after fenestration operations in persons who do not suffer also from nerve deafness, and it is probable that in them the hearing depends upon the pressure difference between the windows.

From a physical point of view it is puzzling that the pressure difference between the two windows can be of the same order of magnitude as the sound pressure in the meatus. The anatomical conditions suggest that the cavities of the mastoid process and the surrounding bones may be responsible. Unfortunately the pneumatization varies so greatly in different temporal bones that it is difficult to arrive at any general conclusion. It can be stated, however, that the hearing losses increase with decreasing pneumatization. From Fig. 5-28 it may be seen that the round window is in the direct path of the sound from the meatus, whereas the artificial opening is situated at the mouth of a large resonance chamber formed by a part of the middle-ear cavity and by air cells of

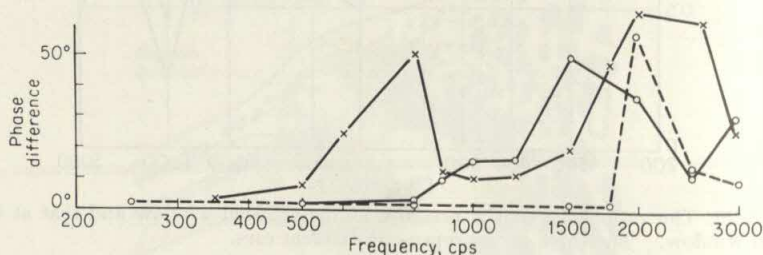


FIG. 5-31. The phase differences between the pressures at round and artificial windows for the three specimens shown in Fig. 5-30.

the mastoid process. It is through this difference of location that the pressure difference between the two windows arises.

Measurements on a Model to Show the Effect of Pneumatization. A model of the middle ear was made, as shown in Fig. 5-32. It consisted of a plate 2 mm thick with two openings 12 mm in diameter. The openings were connected by an isthmus 6 mm long and 3 mm wide. A cover contained a simulated round window placed over one opening and an artificial window over the isthmus. To one opening was connected a tube representing the external meatus, and to the other an adjustable resonance chamber with a volume V representing the cavity of the mastoid process. It was hoped in this way to simulate the main resonance chambers of the ear.

The pressure ratios obtained with this model, for two different volumes of the mastoid process, are shown in Fig. 5-33. If a small piece of cotton was placed in the adjustable cavity, the resonance curve was flattened and curves were obtained similar to those of Figs. 5-30 and 5-31. Thus the behavior of the actual temporal bone could be imitated perfectly. If the whole cavity was filled with cotton, the resonance ceased and the pressure difference between the two windows became small, with a total hearing loss of 60 db for the whole frequency range.

As the resonance was at 1500 cps when the mastoid cavity was given a

volume of 1 cu cm, it can be expected that when the middle-ear cavity is enlarged by surgery the sensitivity will be even greater for the low frequencies. The clinical implications are obvious.

Previous measurements of the impedance of the auditory meatus at low frequencies (10 to 50 cps) showed that for a normal ear the volume of the middle ear was 2 cu cm. This figure agrees well with the present

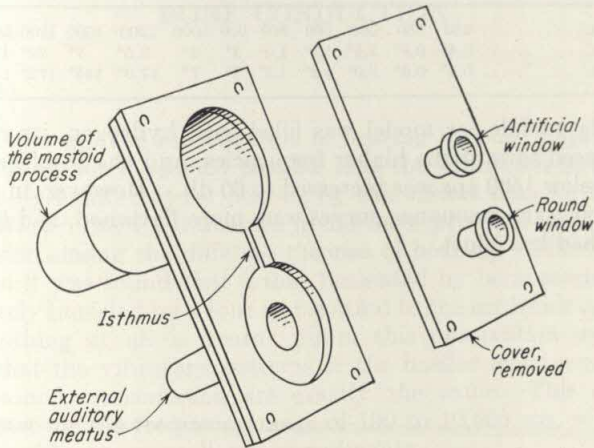


FIG. 5-32. A model of the middle ear and the mastoid cavities.

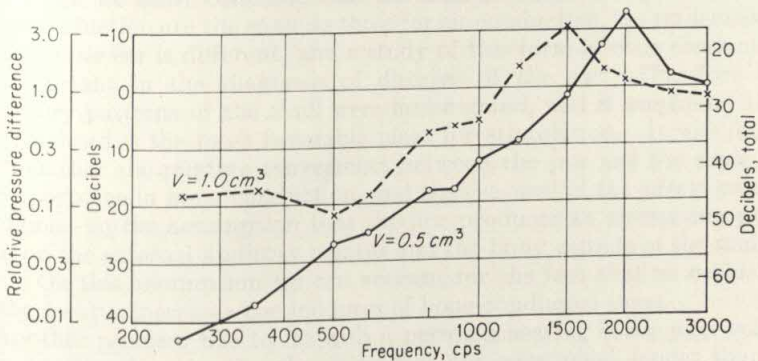


FIG. 5-33. Results obtained on the middle-ear model, expressed as $\Delta p/p$ (left-hand ordinate), in decibels (second ordinate), and as a total loss of hearing in decibels (right-hand ordinate).

observations. At low frequencies the pneumatization of the mastoid process can be measured directly, since the eardrum has only a slight effect on the impedance at these frequencies. It is not possible, however, to draw any conclusions regarding the pressure differences to be expected after a fenestration operation from the degree of pneumatization only, because the magnitude of the isthmus is also of importance.

The middle-ear model showed phase differences between the round and artificial windows. These are given in degrees in Table 5-2 for two

different sizes of the mastoid cavity. The small values of phase were calculated by use of Eqs. (5-1) and (5-2) and the larger ones from the equation $\tan \alpha/2 = 1/\omega CR$. If ωC is kept constant for various frequencies, the phase is the same for a given value of R , and a table can be used for systematic measurements.

TABLE 5-2

Frequency, cps.....	250	350	500	600	800	900	1000	1200	1500	1800	2000	2500	3000
$V = 0.5$ cu cm.....	0.4°	0.6°	2.5°	1.2°	1.0°	3°	3°	3.5°	7°	29°	134°	105°	95°
$V = 1.0$ cu cm.....	0.4°	0.6°	2.0°	1.2°	1.5°	6°	7°	17.0°	145°	172°	150°	13°	4°

When the middle-ear model was filled with hydrogen, its resonances were displaced toward the higher frequencies, and the total hearing loss for tones below 1500 cps was increased to 60 db. However, in the actual temporal bone the resonance curves were more flattened, and filling with hydrogen had less effect.

CHAPTER 6

BONE CONDUCTION

A few years ago the investigation of hearing by bone conduction was very promising, for it seemed possible that the vibrations of the basilar membrane were different for hearing by this means than for hearing by air conduction. Such a difference would have provided an opportunity for a decision among the different theories of hearing. This hope faded away when it was found that a tone presented by bone conduction can be completely canceled by a tone transmitted to the ear by air conduction, so that nothing at all is heard. From this observation we have to conclude that the vibratory patterns of the basilar membrane for both types of sound transmission are exactly the same. This conclusion holds at least for the frequency range of 100 to 10,000 cps, which is the range covered by the cancellation experiments.

Though we must conclude that the final processes of stimulation by bone conduction are the same as those for air conduction, the transmission to the inner ear is different, and a study of this form of bone conduction is important in the diagnosis of diseases of the ear. Therefore the vibratory patterns of the skull were investigated, and it was found that the forehead is the most favorable place for stimulation. It was found further that the relative movements between the jaw and the skull are of importance in bone conduction, and that several of the effects can be explained on the assumption that the jaw produces an alternating pressure on the external auditory meatus and the bony capsule of the middle ear. On this assumption we can account for the fact that an occlusion of the meatus increases the loudness of bone-conducted tones.

Another problem has to do with a person's hearing of his own voice. The question here is why the voice does not seem much louder than it does, in view of the fact that the vibrations of the throat are very large, which can easily be noted on touching the larynx. It was found that the attachment of the middle-ear ossicles and the distribution of their mass is such as greatly to reduce the sound transmitted from the throat to the inner ear. This reduction is not complete, however, and in some degree the voice is heard by bone conduction. When a person hears his voice as recorded by phonograph, it sounds strange to him, because the recording includes only the aerial waves, whereas he is accustomed to hearing these sounds with bone-conducted vibrations superimposed upon them.

A further matter of practical importance is the maximal attenuation of sound that can be obtained with an earplug. During the Second

World War people in almost every country worked on this problem, and there was general agreement that 35 to 40 db of attenuation in the middle of the frequency range is about the maximum obtainable. No better attenuation can be obtained by a plug in the meatus because a certain amount of sound is transmitted to the skull directly from the air. To determine the theoretical maximum of this attenuation, observations were made of the vibrations of the skull in a free field. The measurements gave new hopes for the design and construction of sound-attenuating devices to be applied to the human head.

NATURE OF BONE CONDUCTION*

A vibrating body can be heard in two different ways. Its movements can be transmitted through the air to the tympanic membrane, or it can be brought into direct contact with the bones of the skull. The following discussion will be concerned with the relations between air and bone conduction.

If the stem of a vibrating tuning fork is pressed against the head and the frequency is within the audible range, the pressure waves produced in the bones of the skull will have wavelengths that are long relative to the distances between the individual sensory cells of the organ of Corti. Hence there can be no noticeable pressure gradient between neighboring sensory cells. Likewise, no changes of salt concentration arise at the cell walls, so that according to the theory of neural excitation discussed elsewhere (page 232) there cannot be any excitation of the sensory cells.

Because a direct stimulation of the sensory cells by compressional waves is unlikely, the whole problem becomes a physical one, namely, to determine how a compressional wave in the skull can produce a displacement of the basilar membrane from its normal position in the cochlea. Only through a local deformation of the basilar membrane can pressure differences arise between neighboring cells.

In order to test this point, an attempt was made to cancel an auditory sensation produced by bone conduction by presenting at the same time an air-conducted tone of the same frequency. If the general compression and rarefaction in the cochlea set up by a bone-conducted tone produced a stimulation of the sensory cells, this stimulation would have the same phase along the whole basilar membrane. On the other hand, an air-conducted tone gives rise in part to a traveling wave along the basilar membrane, so that the phase relations along this membrane are continually varying. Therefore, if it is possible to compensate for a bone-conducted tone by means of an air-conducted tone in such a way that nothing at all is heard, we may be sure that in bone conduction the basilar membrane moves in just the same way as it does in air conduction. That is to say, in both instances the vibrations of the basilar membrane are produced by movements of the fluid near the stapes, and there is no other manner of excitation of the sensory cells.

* Article 11 as listed in the Author's Bibliography. Published in 1932.

The success of a compensation procedure depends upon a high degree of constancy of amplitude and phase relations. In the experiments to be described, a bone-conducted tone was produced by a vibrating rod driven by a vacuum-tube oscillator (*cf.* Schwarz and Bárány). The vibrator was fastened to a freely rotating arm (Fig. 6-1), and a string running over a pulley to a weight gave a constant pressure on the middle of the forehead independent of head position. The same oscillator acting through an attenuator and a phase shifter was connected to two telephone receivers held opposite the ears by a special headband.

It is particularly desirable for the receiver not to press directly on the ears. A wire ring about 8 cm in diameter was fastened to the receiver and spaced about 2 cm in front of it, and this ring was held against the side of the skull. This arrangement gave great constancy of tonal stimulation.

A frequency of 400 cps was used, and the bone-conduction tone was given an intensity of 57 db above threshold. When both air- and bone-conducted tones were presented and these tones were sufficiently free of overtones, it was possible, by suitable adjustments of the amplitude and phase of the air-conducted tone, to cause the bone-conducted tone to disappear completely.

The observation is difficult because it is necessary to make the compensation in both ears at the same time, and the slightest movement of the head or lower jaw changes the adjustments. In some subjects, also, the blood pressure changes the adjustment according to the rhythm of the heartbeat, in such a way that the compensation holds only for particular phases of the heartbeat. For frequencies over 800 cps we pass into the region of resonance of the ossicles, and then the phase adjustments become difficult. For frequencies below 100 cps a tactual sensation at the point of application of the vibrator is perceived along with the bone-conducted tone. If these two sensations are strong and about equal, they can easily be distinguished and separately perceived. But if the bone-conducted stimulation is reduced, the two sensations fuse, and a further reduction of the bone-conducted tone is no longer noticeable. The strength of the tactual sensation relative to that of the auditory sensation is not the same for all positions on the head, and it changes also with the form of the vibrating contact.

Form of Vibration of the Skull. Whenever the skull is set into vibration at any point, standing waves are formed on it because of the relatively great elasticity and density of the bones. By means of a rubber listening tube with one end applied to the vibrating surface the

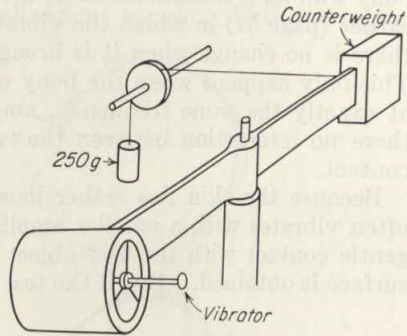


FIG. 6-1. The manner of supporting a vibrator for application to the head at constant pressure.

wave nodes and loops are easily found. With a vibration pickup it may be shown that, at the places where nothing can be heard with the listening tube, the bony surface undergoes no transverse vibrations but only longitudinal ones. To measure the vibratory amplitude of the bony wall for a continuous tone, use may be made of a method described earlier (page 51) in which the vibration of a test object is adjusted until there is no change when it is brought into contact with the bony wall. This only happens when the bony wall and the test object are vibrating at exactly the same frequency, amplitude, and phase, for only then is there no interaction between the two bodies when they are brought in contact.

Because the skin lies rather loosely at many places on the skull, it often vibrates with a smaller amplitude than the bone beneath. For a gentle contact with the test object the vibratory amplitude of the skin surface is obtained. But if the test object is applied more firmly against

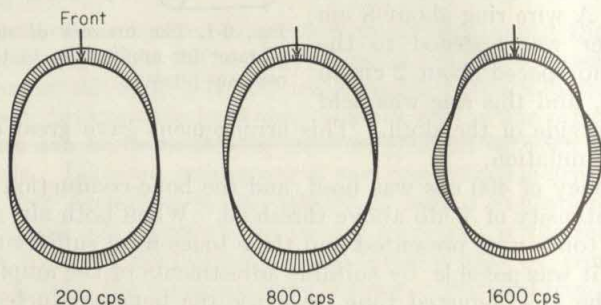


FIG. 6-2. Vibratory amplitudes along the base of the skull when the vibrator was applied to the forehead.

the bone, the skin is compressed and vibrates along with the bone, so that the test object represents the greater vibratory amplitude of the bone. Then when it is taken away its vibratory state is unaltered. If the vibratory amplitude of the test object corresponds to that of the bone, a further increase in the pressure of its application requires no change in the adjustment. For a pressure of 250 grams and a contact surface of 0.5 sq cm the insertion of a piece of sponge rubber 0.5 cm thick between the contact and the head has no effect upon the measurements.

In Figs. 6-2 and 6-3 are shown the amplitudes of transverse vibration of the different regions of the head. The arrow indicates the point of application of the vibrator. Figure 6-4 shows that the four nodes vary in location in a rather uniform way according to the place of application of the vibrator. This observation shows that despite the considerably varying thickness of the skull wall its vibration at low frequencies does not differ appreciably from that of a spherical shell with uniform wall thickness. For frequencies producing six nodes this is no longer true, for in this case a variation in the position of the vibrator usually produces sudden shifts in the location of the nodes.

In order to follow more easily the transition in the form of the vibration during gradual changes of frequency, a white loop of wire was photographed, as shown in Fig. 6-5, when set into vibration by an eccentric device applied at the upper end. For very low frequencies, as for 0.5 cps, there is at first no deformation of any sort, but only a parallel displacement of the loop, whereby two nodal regions appear. With increasing

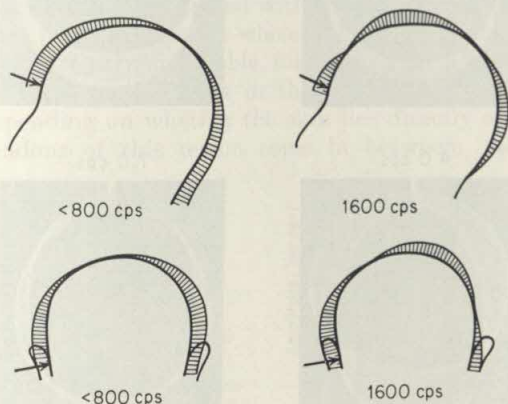


FIG. 6-3. Vibratory amplitudes in the two vertical planes when the vibrations were applied to the forehead or to the mastoid process.

frequency the nodes move downward, on account of the accompanying deformation, until finally two new nodes appear at the upper end. At the same time, the phase of vibration of that side opposite the eccentric suddenly reverses. The same effect is clearly visible in Fig. 6-2. For a further increase in frequency the nodes again move downward, as shown in Fig. 6-5 for a frequency of 9.0 cps. At the transition between two

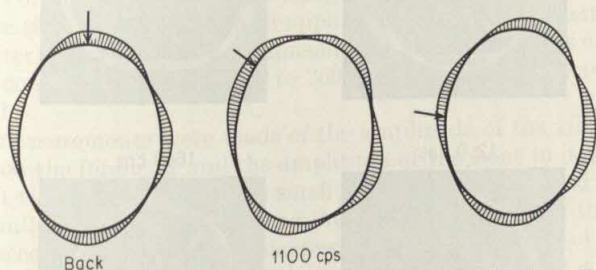


FIG. 6-4. Effects of varying the point of application of the vibrator. The positions of antinodes correspond closely to the point of application.

forms of vibration, traveling waves often appear, and these have the same amplitude around the whole circuit of the loop, as shown for 11.0 cps.

Auditory Threshold Measurements. Because of the appearance of nodes, it is necessary in the measurement of thresholds for bone-conducted tones to take strict account of the points at which the vibrations are applied and the points at which they are measured. The middle of the

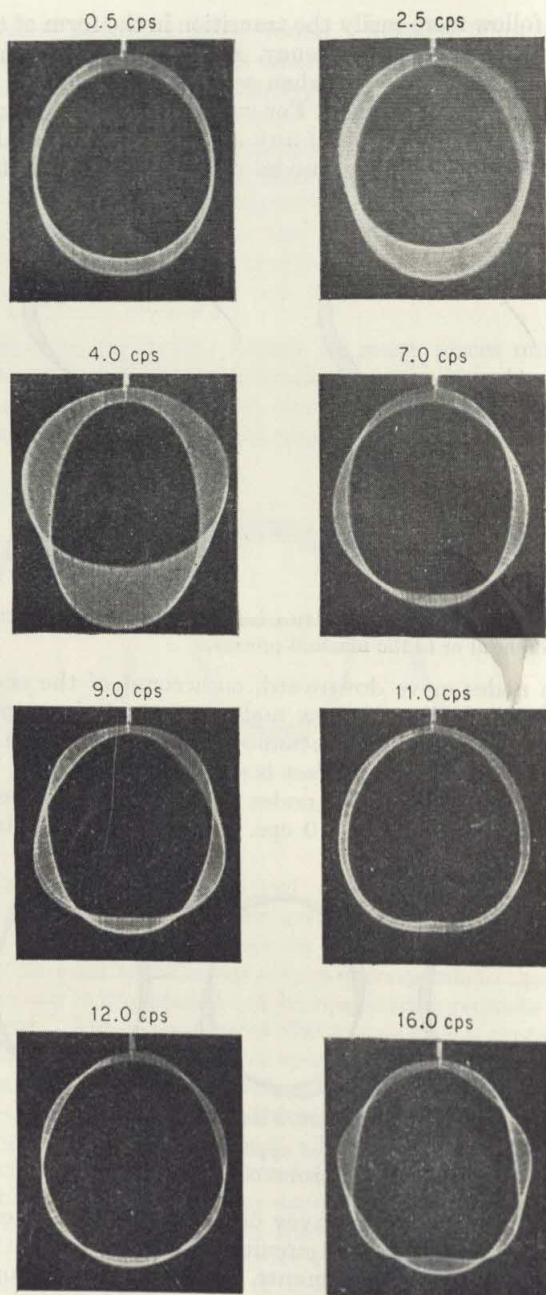


FIG. 6-5. Nodal patterns produced by a vibrating wire loop.

forehead is recommended for standard use because the uniform thickness of the bone here produces a very regular form of vibration, and a shift of the point of application of the vibrator of as much as 3 cm has no effect upon the loudness of the bone-conducted tone. The vibratory amplitude that is transmitted to the bone also should be measured in this same region, preferably at a distance of 2 to 4 cm from the point of application. For the long wavelengths obtained with frequencies up to 2000 cps, the same values are obtained for the whole area around the vibrator. The mastoid process is clearly unsuitable, for here a slight shift in the point of application causes huge changes in the amplitude of the transmitted vibrations, depending on whether the skin lies directly over the bone or the heavy tendons of this region come in between. Besides, on the

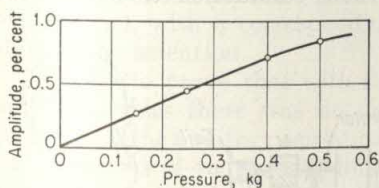


FIG. 6-6. Effects of pressure of application of the vibrator upon the vibratory amplitude of the skull, expressed as a per cent of the applied amplitude, when the vibrator was applied to the skin of the forehead. The vibratory frequency was 800 cps, and the vibrator surface was 50 sq mm.

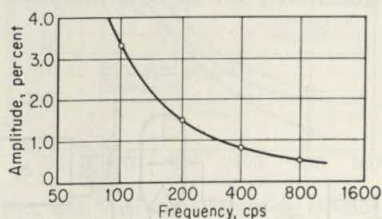


FIG. 6-7. The transmission of vibrations through the skin as a function of frequency. The size of the vibrator surface was 50 sq mm, and the pressure of application was 250 grams.

forehead the tactual sensations that arise at the low frequencies are more easily discriminated from the sounds.

The end of the vibrator is given a slightly rounded form and a diameter of no more than 7 mm, so that an application that is not exactly vertical will not alter the effectiveness of transmission. With this size of vibrating surface a continuous pressure up to 250 grams can be used, as indicated in Fig. 6-1.

When measurements were made of the amplitude of the vibrator when placed upon the forehead and the amplitude of the bone in its immediate vicinity, it was found that only a small fraction of the applied amplitude was transmitted through the skin to the bone, and also that this amount was changed according to the skin thickness. The dependence of the transmission on the pressure of application and on the frequency is shown for one subject in Figs. 6-6 and 6-7.

To test the linearity of transmission through the skin for a contact pressure of 250 grams the arrangement of Fig. 6-8 was used. Here the web of skin between the index finger and the thumb was placed between the electrodynamically driven vibrator and a large mass M . The mass M was so chosen that its mass in relation to that of the vibrator was the same as for the head. The moving coil of an electrodynamic vibrator

was firmly attached to M . Then the electrical potential produced in the coil through its movement was proportional to the amplitude. The potential was compensated for by means of the attenuator b_2 and the phase shifter, so that beyond the two amplifiers and the filter there was a minimum of tone. In order to measure amplitudes as small as 10^{-10} cm at 400 cps it was necessary to use two separate amplifiers with special shielding.

Now it was found that, if the amplitude of the vibrator was shifted by means of attenuator b_1 from 10^{-3} cm down to 10^{-10} cm, the compensating voltage had to be changed in proportion (within a range of precision of 30 per cent). This proportionality between the driving current of the vibrator and the amplitude transmitted through the skin is of great significance, for in determinations of bone-conduction thresholds the

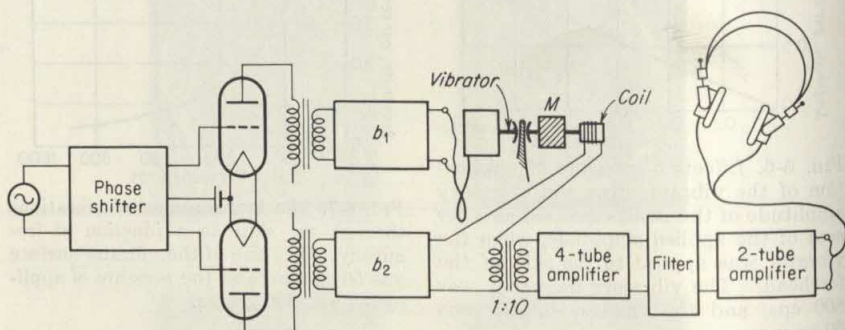


FIG. 6-8. Arrangement for determining the relations between voltage applied to the vibrator and both the amplitude of the vibrator and the vibrations transmitted through the skin.

measurements of the amplitude of vibration of the frontal bone have to be made at a level about ten times greater than the threshold values. The further reduction of amplitude is made with an attenuator in front of the vibrator.

The error of 30 per cent is not significant, for the errors of observation are still greater. In addition to the errors of observation, such as lapses of attention, fatigue, and the like, already well known in threshold measurements by air conduction (Waetzmann and Heisig), there are large variations due to changes in the loudness of the bone-conducted tone caused by shiftings of the lower jaw and from gritting the teeth. These variations are especially large for the low frequencies.

For practical purposes it often is sufficient to determine, as Knudsen and Jones did, the dependence of the threshold upon the amplitude of the vibrator that is applied to the head. But for theoretical reasons this is not enough: the transmission through the skin is subject to large variations according to the form of the vibrator, the pressure of application, and the frequency, and to eliminate these variations it is necessary to measure the vibration of the bone itself.

The short-dashed curve of Fig. 6-9 shows the threshold values of amplitude obtained from the forehead when the external auditory meatus was open. One ear was then loosely closed with a rubber stopper containing a capillary tube. The capillary tube was used to equalize any pressure difference between the meatus and the outside. Then, within the range of tones studied, there was a significant increase in the loudness of the sounds and hence a decrease in the threshold, as shown by the heavy solid curve.

In the first situation the loudness of the bone-conducted tone was the same in the two ears, and the sound image seemed to be in the middle of the head. In the second situation the sound image jumped over to the closed ear (as in Weber's experiment), with a corresponding shift of the attention.

In order to prove that with the low frequencies there was no disturbance of the auditory sensations by sensations of touch, the difference limen for pitch was measured for bone conduction and found to be identical with that for air conduction. For touch this limen had considerably larger values. If there had been a masking of the tonal sensations by the tactual sensations, the difference limen for bone conduction would have been larger. If the amplitude of the vibrator was increased, the tactual sensations finally reached their threshold, whereupon the sound image shifted in the direction of the vibrator.

To make a better comparison of the thresholds for bone and air conduction, an absolute determination was made for air conduction with the same subject and the same arrangement for measuring amplitude.

If the vibrator with a diameter of 0.7 cm, shown in Fig. 6-10, is introduced into the auditory meatus, the air of the meatus is alternately compressed and rarefied, and these pressure variations can be computed from the amplitude of the vibrator and the volume of the meatus (this volume was found to be 0.8 cu cm by filling with water). To avoid any static-pressure changes on introducing the vibrator into the meatus, a glass capillary was cemented into the end as shown. The acoustic impedance of this capillary, whose diameter was 0.02 cm, was so great as not to influence the sound pressure in the meatus. To avoid a lateral flow of air along the vibrator the meatus was smeared with petroleum jelly.

Preliminary measurements proved that the vibrator operated with the same amplitude as the test point at the end of a long rod attached to it. The amplitude was then measured at this point at a level about 20 db above threshold. Finally the amplitude was reduced to the threshold

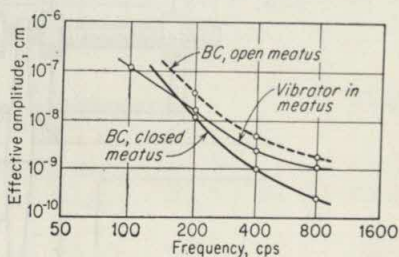


FIG. 6-9. Auditory thresholds obtained for three conditions: for bone conduction with open meatus (short-dashed line), for bone conduction with closed meatus (heavy solid line), and for stimulation with a vibrator in the meatus (light solid line).

value by means of an attenuator that preceded the electrodynamic system. The threshold amplitudes are given by the light solid curve of Fig. 6-9.

Because an incorrect position of the vibrator in the meatus can easily lead to a transmission of the vibrations to the bone, it was always necessary to test whether a loose closure of the other ear, as by the finger, would

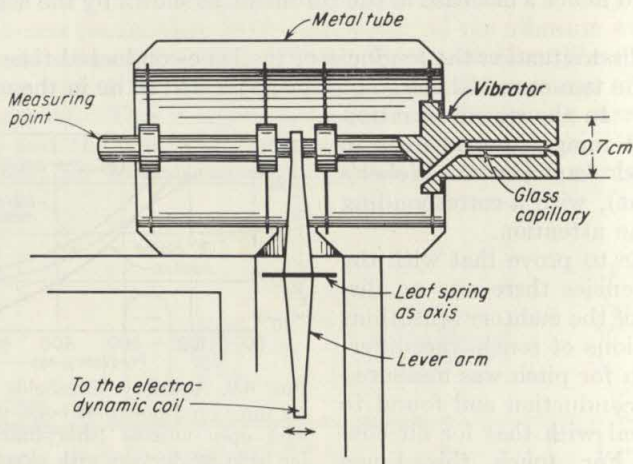


FIG. 6-10. Vibrator for the measurement of air-conduction thresholds.

change the loudness of the sound image. For if a bone-conducted tone is present in noticeable degree, this ear closure, as Fig. 6-9 shows, will cause a marked increase in the loudness of the bone-conducted tone in the ear concerned. In this event the sound image of the air-conducted tone produced by the vibrator will change its form and location, and will be displaced toward the ear that has been closed.

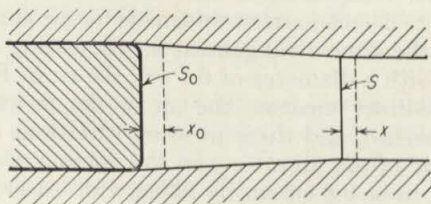


FIG. 6-11. Calculation of the effect on the threshold of the yielding of the eardrum.

In order to determine from the vibratory amplitudes the pressure variations produced by the vibrator in the meatus, let us consider Fig. 6-11. If the object on the left with a cross-sectional area S_0 is shifted to the right a distance x_0 , the eardrum, whose cross-sectional area is S , will be shifted in the same direction by a distance x as it yields to the increased pressure in the meatus. The volume change arising in the meatus as a result of this shift of the object is $dV = Sx - S_0x_0$, where V is the volume of the meatus.

When the shiftings occur at a high frequency we can assume that the volume variations are completely adiabatic, and so the pressure variation is

$$p = -\rho c^2 \frac{dV}{V} = \frac{\rho c^2}{V} S_0 x_0 - \frac{\rho c^2}{V} Sx \quad (6-1)$$

where ρ is the density of the air and c is the speed of sound in a free field. For the frequency range considered here, the dimensions of the meatus are small relative to the wavelengths in a free field.

In agreement with Stewart and Lindsay, we can define the acoustic impedance Z of a system with the opening S as the relation between the pressure p and the rate of volume displacement of the air particles in the opening of the system, or

$$Z = \frac{p}{S dx/dt} \quad (6-2)$$

Then for sinusoidal vibrations with an angular frequency ω , $x = ae^{i\omega t}$, and $Z = p/i\omega Sx$. Hence from Eq. (6-1) we obtain for the pressure variations

$$p = \frac{\rho c^2}{V} S_0 x_0 \frac{1}{1 + \rho c^2/V \times 1/i\omega Z} \quad (6-3)$$

If the ear were acoustically rigid, x would equal 0, and then Z would equal ∞ , so that the quantity on the right side of Eq. (6-3) would equal 1. This quantity then serves as a correction for the acoustic impedance of the eardrum.

Measurements of the impedance of the eardrum were made by Tröger. However, he took as the impedance the relation of pressure to particle velocity, and so his values, as Eq. (6-2) will show, need to be divided by S , the cross-sectional area of the meatus. Since the tube that was used here had a diameter of 7 mm, his values of impedance have to be multiplied by 2.6 to correspond to the present definition.

If we separate the obtained impedance into real and imaginary components, $Z = A + iB$, then the absolute value of the quantity on the right of Eq. (6-3) is

$$\left| 1 + \frac{\rho c^2}{V} \frac{1}{i\omega Z} \right| = \sqrt{\frac{A^2 + (B - \rho c^2/V\omega)^2}{A^2 + B^2}}$$

If we put into this equation $\rho = 1.2 \times 10^{-3}$, $c = 3.4 \times 10^4$ cm per sec, $V = 0.8$ cu cm, and for A and B the corrected values obtained by Tröger for one subject (as given on page 38 of his paper), then for the different frequencies we obtain the values shown in Table 6-1.

TABLE 6-1

Frequency, cps.....	250	450	800	1000	1500	3000
$1 + \frac{\rho c^2}{V} \times \frac{1}{i\omega Z}$	2.8	2.7	3.5	1.7	2.0	1.4

Above 800 cps, on account of resonances of the membrane as a whole and of its separate parts, the results are highly variable, but they average about 1.6.

We see from these figures that the sound pressure in the meatus is reduced by the yielding of the eardrum by a maximum of about 3.5-fold (compare with the results of Langenbeck and of Waetzmann and Heisig). This yielding of the eardrum seems very large, because for a threefold reduction of sound pressure the volume displacement of the eardrum is only about 33 per cent smaller than that of the vibrator, in spite of the easy compressibility of the air of the meatus. Nevertheless, in auditory threshold measurements with the thermophone the compliance of the eardrum plays a minor role, because usually in this situation the volume V is very large.

If from the data of Fig. 6-9 and Eq. (6-3) we calculate the threshold for air conduction, we obtain the results of Table 6-2. These values agree well with those of E. Meyer (6).

TABLE 6-2

Frequency, cps.....	100	200	400	800
Effective pressure, dynes per sq cm $\times 10^{-4}$	270	40	5.9	2.2

The capillary in the vibrator had a radius of 10^{-2} cm and a length of 1.0 cm. Here, as Crandall found, the frictional force in the tube is so great that the mass reactance of the vibrating air column can be neglected. Therefore, according to Poiseuille's law, the rate of flow of the gas in the tube, in volume per unit of time, is

$$S \frac{dx}{dt} = \frac{\pi r^4 p}{8 \mu l}$$

where $\mu = 1.87 \times 10^{-4}$ cgs units is the frictional coefficient of the air, l is the length of the tube, and r is the internal radius of the tube. The acoustic impedance of this system, from Eq. (6-2), is

$$Z = \frac{8\mu l}{\pi r^4} = 48,000 \text{ cgs units}$$

Thus the impedance of the capillary relative to the eardrum impedance even for low frequencies is so great that the capillary has no effect upon the measurements. Smearing with petroleum jelly ensured against any other openings.

Knudsen and Jones have already found that a noise has less effect on the auditory threshold for bone conduction than for air conduction. This happens because in air conduction, with a telephone receiver over the ear, the sound image of the air-conducted tone usually coincides with that of the noise. The presence of the receiver on the ear prevents any impression of distance for the noise, and it therefore is localized in the immediate vicinity of the meatus. For bone conduction, on the other hand, the

sound image of the bone-conducted tone seems to be in the middle of the head and completely separate from the noise image outside the head. Because of the spatial separation the two are easy to distinguish.

Figure 6-12 shows the extent to which the auditory threshold is raised for air-conducted tones and for bone-conducted tones of various frequencies when they are masked by an aerial tone of 900 cps at a loudness

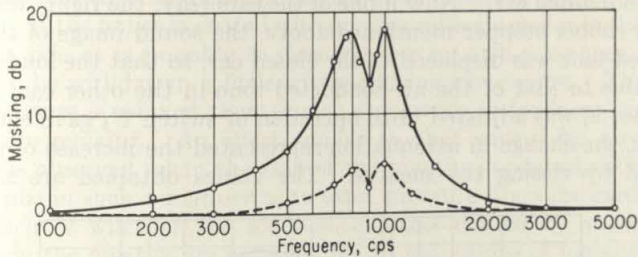


FIG. 6-12. The masking effect of an aerial tone of 900 cps in one ear as observed for various air-conducted tones in the same ear (solid-lined curve) and for bone conduction with the vibrator applied to the forehead (broken line).

of 40 db above threshold. The masking tone was presented by means of a telephone receiver 2 cm from the ear. Though the air-conducted tone showed masking, corresponding to the measurements of Wegel and Lane, the bone-conducted tone applied to the forehead was but slightly masked by an aerial tone on the same side, because the bone-conducted tone was heard also with nearly equal loudness in the other ear.

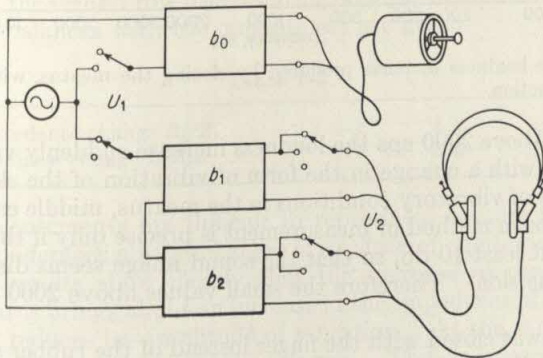


FIG. 6-13. Arrangement for measuring the increase in loudness produced by closing the meatus.

Sound Perception with Closed Meatus. The following arrangement (Fig. 6-13) was used to measure more precisely the increase of loudness of a bone-conducted tone produced by closing the meatus. Telephone receivers were placed over both ears, supported about 2 cm away from the head. The attenuator b_1 and the switch U_2 were adjusted so that the air-conducted tone seemed to be in the median plane of the head. It was necessary also to have the correct phase for the two receivers. For

the bone-conducted tone a point on the forehead was chosen so that its sound image with the ears open was indistinguishable from that of the air-conducted tone. Attenuator b_0 was adjusted so that equal loudness was obtained on switching back and forth with U_1 . Whenever the two sound images were equally loud and had the same direction, the loudness of the bone-conducted tone was equal to that of the air-conducted tone in each individual ear. Now if one of the ears (say, the right) was closed with the rubber stopper mentioned above, the sound image of the bone-conducted tone was displaced to the closed ear, so that the loudness was comparable to that of the air-conducted tone in the other ear. If now attenuator b_1 was adjusted until operation of switch U_1 gave equality of loudness, the change in attenuation represented the increase of loudness produced by closing the meatus. The values obtained are shown in

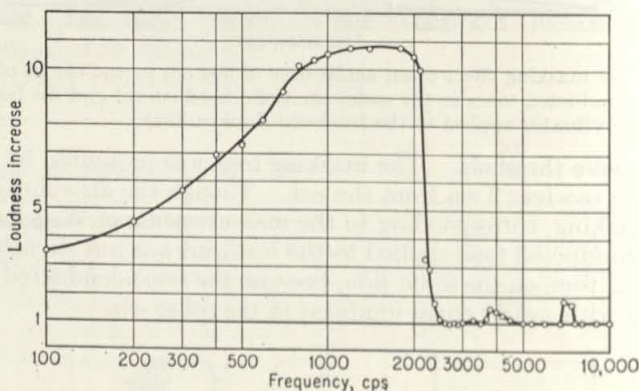


FIG. 6-14. The loudness increase produced by closing the meatus, with stimulation by bone conduction.

Fig. 6-14. Above 2000 cps the loudness increase suddenly vanishes; this is correlated with a change in the form of vibration of the skull and also with changes of vibratory conditions in the meatus, middle ear, and inner ear. The above method of measurement is precise only if the increase of loudness is at least 10 db, so that the sound image seems displaced completely to one side. Therefore the small values above 2000 cps are only estimated.

If the ear was closed with the finger instead of the rubber stopper with its capillary, the same increases of loudness were observed when closure was loose, but decrease of loudness occurred when closure was firm.

Mach (1; see also Schaefer and Giesswein) was the first to give a thoroughgoing presentation of this problem. In his "sound-outflow theory" he supposed that the decrease in loudness arose from the firm pressing of the finger on the skull, which allowed the sound to flow out through the finger.

It is easy to show that the firm attachment of a large mass of lead to the forehead has only a slight effect upon the loudness of a bone-conducted tone applied to the forehead. The reason, as Fig. 6-7 shows, is that, for

the high frequencies especially, the skin layer prevents any damping of the skull vibrations by the lead mass. Probably the decrease in loudness occurs because the finger when strongly pressed into the meatus changes the air pressure from its normal value and thereby displaces the ossicles from their usual positions and diminishes their mobility.

The following experiment shows that the changes of air pressure are significant and that in this instance the sound-outflow theory cannot be applied. If the finger is coated with grease and is pushed into the meatus from one side, it is possible to close the ear in such a manner that the finger can be withdrawn a little without losing the closure. Then if the finger pressure is relaxed there is also a decrease in loudness, as long as the closure remains. An effect similar to that caused by air-pressure changes is observed when the skin of the meatus is pushed with a short plastic tube in such a manner as to exert pressure upon the eardrum.

To discover whether the loudness changes caused by variations of pressure in the meatus are actually due to reductions of mobility of the eardrum and ossicles, the alterations of impedance of the eardrum were measured. As Eq. (6-2) shows, a reduction of mobility is accompanied by an increase in the impedance of the eardrum.

The impedance of the eardrum was found by a substitution method* like that described on page 69. This method can only be carried out for frequencies below 800 cps, for which the eardrum vibrates as a whole. Results obtained for a tone of 400 cps are shown in Table 6-3. In the first row of the table are given, for three different subjects, the relative changes in impedance produced by a static pressure rise of 10 cm of water; and then, in the second row, the resulting changes of loudness as obtained by loudness balances with the opposite ear are given.

TABLE 6-3

Impedance change Z_h/Z_0	2.1	1.8	1.5
Loudness change L_0/L_h	2.7	2.0	1.35

These measurements are difficult to reproduce, because the ossicular chain often undergoes abrupt changes in its state of equilibrium. Nevertheless, the results show clearly that the increase of pressure in the external meatus brings about an increase in the impedance of the eardrum and thereby reduces its amplitude of vibration. At the same time, the loudness is reduced in corresponding degree. Thus it is established that the loudness changes have a mechanical cause, and the assumption often made that there is a change in neural sensitivity as a result of an increase of pressure in the cochlear fluid is unnecessary.

A complete correspondence between the impedance changes and the loudness changes is not to be expected, because the coupling between the eardrum and the ossicles is close for only a portion of the eardrum. The lateral region of the eardrum (the membrana flaccida) vibrates more or less independently of the main region, and a pressure increase in the

* *Ann. Physik.*, 1932, 13, 126-127.

meatus probably alters its impedance in a different way, as observation with the ear microscope indicates.

For a reduction of static pressure there is correspondingly a reduction of loudness and a rise in the eardrum impedance.

The arrangement of Fig. 6-15 was used to permit a better comparison of the loudness changes produced in air-conducted and in bone-conducted tones by a variation in the pressure in the meatus when the meatus was closed. The vertical stem of a T tube that was connected to an air pump was adjusted below the surface of the fluid in a vessel as shown so that when the stopcock was closed a certain pressure was present in the system. This pressure was indicated by a manometer. A telephone receiver

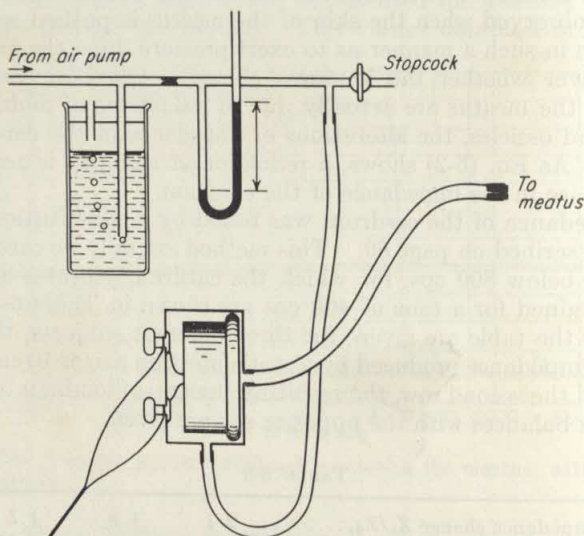


FIG. 6-15. Method for measuring the effects of pressure changes in the meatus on loudness.

enclosed in a metal chamber was so arranged that the air could reach both sides of its diaphragm equally well in order to avoid any effect of the pressure changes upon the sound output of the receiver. The rubber tube leading to the meatus was provided with a small capillary at its end, and this end was connected to the meatus. It is important that the tube make an airtight seal in the meatus, so that there is no flow of air through the capillary. Such a flow through the capillary will greatly reduce the sound produced by the receiver. For this reason the inside diameter of the capillary was no smaller than 0.5 mm.

An alternate-comparison method was used to determine the loudness changes produced by variations of air pressure for an air-conducted tone. The stopcock was automatically opened and closed, and at the same time the telephone receiver was alternately connected to an oscillator through two different attenuators. The attenuators were adjusted so that during

this switching no change of loudness was observed. The difference in their settings then gave the desired loudness changes.

For this study of the effects on bone-conducted tones, the telephone receiver was shorted and a vibrator was applied to the head so as to produce a tone of the same frequency and loudness. Then, because the tube remained in the meatus, the sound image was referred to this ear just as with the air-conducted tone. In addition, the low frequencies gave a tactual sensation at the point of application of the vibrator, and this sensation of course did not vary in intensity when pressure changes were introduced. For higher frequencies, especially when a proper choice was made of the point of application of the vibrator, the tactual sensations were so much diminished that they were no longer disturbing. Under these conditions the loudness changes resulting from variations of pressure were measured by the alternate-comparison method as before.

Under these conditions, extensive measurements were carried out for 400 and 800 cps, with both increases and decreases of pressure, and it was found that the loudness changes with closed meatus were exactly the same for air conduction and for bone conduction, provided that these changes did not exceed 10 db. When the changes were greater than this the sound image of the bone-conducted tone was no longer localized in the meatus.

The fact that the sound image of a bone-conducted tone as heard with closed meatus has the same form and position as that produced by an aerial tone heard through a tube, as in Fig. 6-15, shows that with closed meatus the tone produced by bone conduction arises mainly as a result of variation of air pressure in the meatus. Only on this basis can we understand why a fixation of the stapes has the same effect upon the two modes of conduction, and only in this manner can we account for the large increase in loudness caused by closing the meatus.

If the telephone receiver shown in Fig. 6-15 is used as a microphone, it can be shown that an increase of static pressure in the closed meatus produces an increase in the sound pressure in the meatus resulting from a bone-conducted tone. This can only be explained if the sound pressure in the meatus is caused by a contraction of the meatal walls. In this case the increase in the impedance of the eardrum will give a larger sound pressure for a given volume displacement of the meatal walls.

Also to be considered as a source of sound pressure in the meatus are vibrations of the end of the lower jaw. If the lower jaw is moved while the finger is inserted in the meatus, a displacement of the cartilage in the canal is easily felt. This is the displacement that gives rise to the volume changes. Also, direct measurements will show that when the skull is vibrating the lower jaw does not follow it exactly. There are phase differences between the movements of skull and mandible. Figure 6-16, which presents a longitudinal section through the meatus when the mouth is closed, shows why this situation is to be expected on anatomical grounds.

It should be noted further that the vibration of the end of the mandibular joint will produce much less compression of the middle-ear region than of the meatus, because of the presence of a thin but relatively rigid bony

plate between this joint and the middle ear. The plate of cartilage bounding the meatus, on the other hand, is easily movable. If the end of the joint is shifted outward, which is easily accomplished by a lateral movement of the jaw, the wall of the meatus will then more readily follow the movements of the end of the joint. Now it can be observed, especially for low tones and when the meatus is closed, that the outward

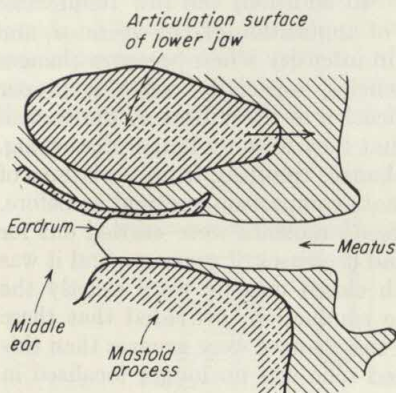


Fig. 6-16. A longitudinal section through the meatus, inclined about 45° to the vertical plane.

displacement of the joint produces a sharp increase in loudness. This is true regardless of whether the vibrator is applied to the side of the jaw or is placed on the mastoid process so as to produce lateral vibrations of the head.

If the teeth are clamped firmly together the relative movements between the lower jaw and the skull are reduced, and there is a decrease in the loudness of the sound. The loudness changes are most prominent for the high frequencies and for vibratory movements of the end of the mandible that are not parallel to the axis of the meatus. Then the mandible

does not vibrate simply back and forth but undergoes rotations. Accordingly, the movements are damped by the surrounding portions of the articular capsule in various and complicated ways.

It is possible to set the lower jaw into lateral vibration by applying the vibrator to it, but without producing any vibrations of the head, as may be proved by the use of a vibration pickup. Then it is found that with closed meatus the threshold amplitude of the jaw vibrations is much smaller than the threshold amplitude of the vibrator that is inserted into the meatus. Evidently a given amplitude of vibration of the jaw produces significantly greater volume displacement in the meatus than does the vibrator working in the meatus directly. Therefore it is understandable why, as Fig. 6-9 shows, the threshold for bone conduction with the ear closed is below that for the vibrator in the meatus.

Bone Conduction with Open Meatus. The situation is entirely different when the meatus is open. The compressions in the meatus can exert only slight pressures on the eardrum, and the relative displacements of the ossicles and the compressions in the cochlea can be of importance. In support of this is the fact that the lower jaw because of its inertia will vibrate with different amplitude and phase from the adjoining bones, so that it exerts only a localized force upon the skull in the immediate region of the cochlea. Therefore the loudness with open meatus may change a little when the lower jaw is displaced.

The vibrations produced by bone conduction can roughly be resolved into parallel, compressional, and rotational vibrations of the cochlea and

middle ear. The rotational vibrations will be neglected, for the observed phenomena are fully accounted for by the other two kinds. If the rotational vibrations produced an appreciable displacement of the basilar membrane, its form of motion would be entirely different from that produced by the vibrations of the stapes, and the compensation of a bone-conducted tone by an air-conducted tone would not be possible.

Because of the inertia of the ossicles, the parallel form of displacement acts on the middle ear so as to produce a vibratory force upon the stapes. For low frequencies this force is nearly opposite in phase to the vibrations of the middle ear and meatus.

Rejtö and Herzog pointed out that if there is equality of all elastic characteristics in the two cochlear scalae, then a compression of the cochlea will produce the same pressures and fluid displacements on both sides of the basilar membrane. Therefore the basilar membrane will not undergo any displacement, as indicated in *a* of Fig. 6-17. But in actuality, the mobility of the stapedial footplate is much less than that of the round window, and therefore, as *b* of this figure shows, there is a displacement of the basilar membrane that becomes greater as the difference in mobility of the two windows is increased. On this basis we can explain the often-observed fact that a complete fixation of the stapes to the cochlear wall abolishes hearing by air conduction, while it produces only a limited change in the thresholds for bone conduction. The asymmetry between the two cochlear scalae is increased, as *c* of Fig. 6-17 indicates, by the presence of the vestibule and semicircular canals in the region of the stapes, and their compression can produce a significant displacement of fluid near the stapes. Perhaps also this action is enhanced further by fluid squeezed out of the blood vessels.

It is now important to show that compression in the cochlea has an important effect upon bone-conducted tones with open meatus.

If a bone-conducted tone is completely canceled by an air-conducted tone so that the basilar membrane is not moving, the stapes must have an outward movement that is equivalent to the fluid that is pushed into the upper scala of the cochlea because of the compression effect.

If there is no compression of the cochlea, then during the compensation the stapes will not move in its window. Then if the static pressure in the external meatus is altered and the stapes is fixed, there will be no change. But if there is a compression of the cochlea, a reduction in the mobility of the stapes will produce an increase in loudness. If after the introduction of the static pressure the compensation is carried out once more, the

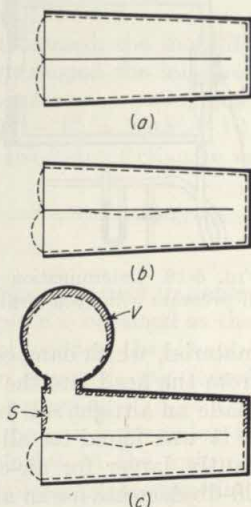


FIG. 6-17. Effects on the basilar membrane of compressions of the cochlea.

reduced mobility of the stapes makes it necessary to use a larger sound pressure than before in order to produce the compensation.

The last two conclusions are well established. The complete compensation of the fluid movements is achieved because the opening of the vestibule and canals lies close to the stapes.

Though it is found with closed meatus that a static-pressure increase produces the same decrease in loudness for air-conducted tones as for bone-conducted tones, it is probable that with open meatus the compression in the meatus is of little importance. Also the inward displacement of the stapes that is caused by compression of the middle ear is of the same order of magnitude as the fluid that is simultaneously forced from

the vestibule and canals into the upper scala of the cochlea. It is therefore to be expected that the loudness of the bone-conducted tone will be less affected than that of the air-conducted tone, because the fluid flowing in from the vestibule and semicircular canals is not changed.

The arrangement shown in Fig. 6-18 was used to study the effects of static pressure in the open meatus. The ear was completely free in a large pressure chamber whose walls

were lined with sound-absorbing material, which damped the transmitted and radiated vibrations coming from the head into the chamber. A fluid-soaked layer of sponge rubber made an airtight seal between the chamber and the head.

It was found for all subjects that the loudness changes were significantly larger for air-conducted tones. Thus a pressure that gave a 20-db decrease for an air-conducted tone gave only a 10-db decrease for a bone-conducted tone.

In a few subjects it was even possible, by a proper choice of the point of application of the vibrator, to cause such a reduction in the tone arising in the middle ear with open meatus that a 10-db increase in loudness was perceived for a pressure increase of 20 cm of water. Also in the normal ear it was possible to confirm the usual clinical observation that a reduction in the mobility of the stapes increases the loudness of a bone-conducted tone.

It is frequently found also that tones above 3000 cps, which often do not show any loudness increase when the meatus is closed, as Fig. 6-14 has indicated, and thus do not set up any appreciable pressure variations in the meatus, nevertheless undergo clear increases of loudness when the finger is pressed firmly into the meatus.

An increase of loudness occasionally occurs when the vibrator is on the lower jaw and the air pressure in the meatus is increased by means of the

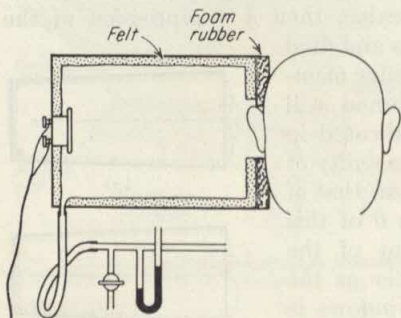


FIG. 6-18. Determination of the effects of pressure with open meatus.

pressure chamber over the ear. With a lateral displacement of the lower jaw, which causes a compression of a larger portion of the meatus, there is a decrease of loudness.

With the meatus open we can also determine the relation of the volume displacement caused by compression in the vestibule and semicircular canals and the upper scala of the cochlea (shown as crosshatched in *c* of Fig. 6-17) to the volume displacement caused by movements of the stapes.

If we let V represent the volume reduction resulting from compression of the vestibule and semicircular canals and the upper scala of the cochlea and let S represent the similar volume reduction caused by displacement of the stapes, then according to Fig. 6-17*c* the loudness L of a bone-conducted tone is determined by the yielding of the basilar membrane, or $S + V$. If k is a proportionality factor, then $L = k(S + V)$. In the situation represented by Fig. 6-17*a*, S is negative and equal to the volume change in the upper scala of the cochlea, so that $S + V = 0$.

If now the pressure in the external meatus is increased, the mobility of the stapes will be diminished by a factor n , whereupon the loudness will change by the factor N . If we represent values for pressure increase by primes, then $S' = nS$ and $L' = NL = Nk(S + V) = k(nS + V)$. From this equation we derive the relation of the two volume changes as

$$\frac{V}{S} = \frac{N - n}{1 - N}$$

The loudness change N produced by a pressure change is easy to determine, whereas the reduction of mobility of the stapes n is obtained as the loudness decrease of an air-conducted tone of equal loudness that is subjected to the same increase in static pressure. In general it was found that $n = 0.3$ and $N = 0.7$. The volume relation then is $V/S = 1.3$. The fact that despite the density of the petrous bone a large value is obtained for the compression of the cochlea relative to the volume displacements of the stapes is in part due to the small size of the stapedial footplate, which even for large displacements produces only small volume changes. Perhaps the fluid of the blood vessels is pushed into the cochlea also. These relations, however, vary according to the position of the lower jaw.

If, with open meatus and a proper choice of the point of application of the vibrator, the compression in the middle ear is so small that the volume changes of the vestibule and semicircular canals cause an outward displacement of the stapes, then a fixation of the stapes always produces an increase in loudness.

According to earlier assumptions the stapes is always displaced outward by a compression in the cochlea. Then the stapedial vibrations would be transmitted to the eardrum, and its movements would produce a sound pressure in the meatus. That this assumption is incorrect is shown by the observation that after the stapes and other ossicles were removed in a cadaver the sound pressure in the closed meatus was not altered.

ABSOLUTE BONE-CONDUCTION THRESHOLD*

First to be considered are the various possibilities for measuring the absolute threshold for bone-conducted sounds. The vibrations of a solid body, such as a tuning fork, may be heard in two different ways. One way is by its action on the air and the transmission of the aerial vibrations to the ear, which is called air conduction. The other way is through a contact with the bones of the skull, as by placing the stem of the tuning fork on the forehead, which is called bone conduction. These two ways of transmitting sound to the inner ear are not exactly the same, and their use provides the otologist with a means of ascertaining the seat of an auditory impairment.

Thus if the otologist himself, who presumably has normal hearing, perceives a vibrating tuning fork by bone conduction for a longer time than the patient does, then it is probable that the patient suffers from an impairment of the inner ear. If on the other hand the patient hears the fork for a longer time than normal, a middle-ear impairment is indicated. This is the Schwabach test. If a fork is heard for a longer time by air conduction than by bone conduction, an inner-ear defect is indicated, whereas if the reverse is true the middle ear is involved. This is the Rinne test. These and similar observations depend always on the thresholds for air and bone conduction.

Though these clinical tests have been used for many decades and an almost unbelievable number of articles have been written about them, a great many questions concerning them remain unsolved. Often the different tests give conflicting results, and only a consideration of the total picture will indicate whether, for example, an inflammatory process in the ear is active or not. Extensive experience is necessary for a proper evaluation of the various results, and account must be taken of the special characteristics of the tuning fork being used and the room noise that is present during the tests.

A precise determination of auditory thresholds by air and bone conduction ought to contribute to the decision as to whether an impairment of the ear is purely conductive or not. Though the threshold by air conduction has been studied extensively and in a precise manner, especially by Waetzmann and Keibs and by Kurtz, a similar degree of precision has not been attained for bone conduction. The measurements made by Knudsen and Jones and by Watson, for example, referred simply to the amplitude of a vibrating body that was just perceptible when applied to the head. Because the skin is highly variable, there are great difficulties in obtaining absolute measurements. A method must be found for measuring the vibrations communicated through the skin to the bones of the head.

To study the variability of the skin's properties, measurements were made of the thickness of the web of skin between forefinger and thumb when exposed to a steady pressure of 1 kg over a period of time. Figure

* Article 31 as listed in the Author's Bibliography. Published in 1939.

6-19 shows these results. Also, Fig. 6-20 shows how the compression of the skin varies with the applied pressure. In these measurements the pressure was first increased by steps to a value of 1500 grams (solid line) and was then reduced to the initial value (broken line). A large and

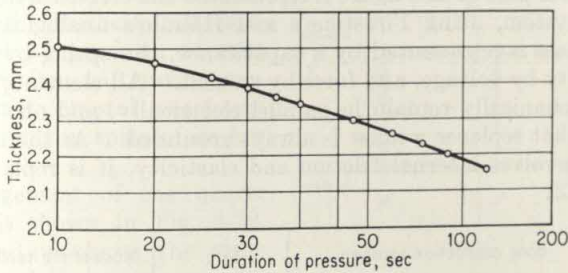


FIG. 6-19. The progressive thinning of the skin when exposed to a pressure of 1 kg. The skin area was 0.8 sq cm.

lasting residual effect is obvious. It may be seen from the solid curve that a pressure increase from 0.1 to 1.5 kg causes an increase in the modulus of elasticity by tenfold.

To determine in an exact way the vibrations of the bone at a particular point on the head, measurements may be made of either the amplitude of the bone or the pressure acting upon it. In an earlier study (page 51) a probe method was described for determining the amplitude of the bone despite the presence of the skin. (The sensitivity of this method may be improved by mounting a crystal or condenser microphone at the end of the probe and using it to obtain uniform amplitudes.) Here the measurement of pressures will be investigated, because such measurements appear to be more practical for bone-conduction thresholds.

The vibratory system shown in the upper part of Fig. 6-21 was used to study the possibilities of measuring the transmission of sound pressure to the bones of the head independently of the properties of the skin. This system consists of a bone-conduction receiver, the skin, and the mass of the head, schematically represented. M_1 is the mass of the electro-magnet that is connected to M_2 , the mass of the vibrating body, through a spring. Parallel to the spring a frictional force is represented. The

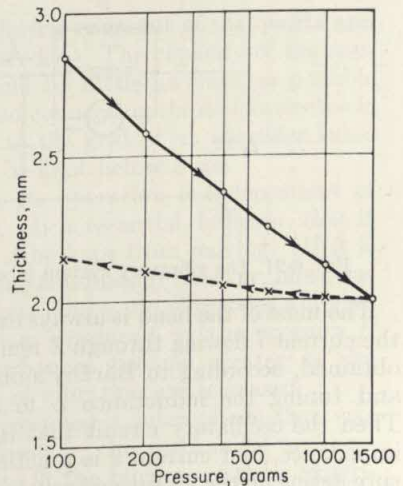


FIG. 6-20. Effects of increasing and decreasing the pressure on the skin. The skin area was 0.8 sq cm. The arrows indicate the order of application.

driving force of the receiver is represented by f . The elastic properties of the skin are represented by the massless spring, whose magnitude is variable. The mass of the head is represented schematically by the mass M_3 .

In the lower part of this figure is represented the electrical analog of the vibratory system, using Firestone's and Hähnle's analogical relations. Here the mass is represented by a capacitance, the spring by an inductance, velocity by voltage, and force by current. All elements that are in parallel mechanically remain in parallel electrically, and one side of the condenser that replaces a mass is always grounded. As the mass of the head also involves internal friction and elasticity, it is replaced by the impedance Z .

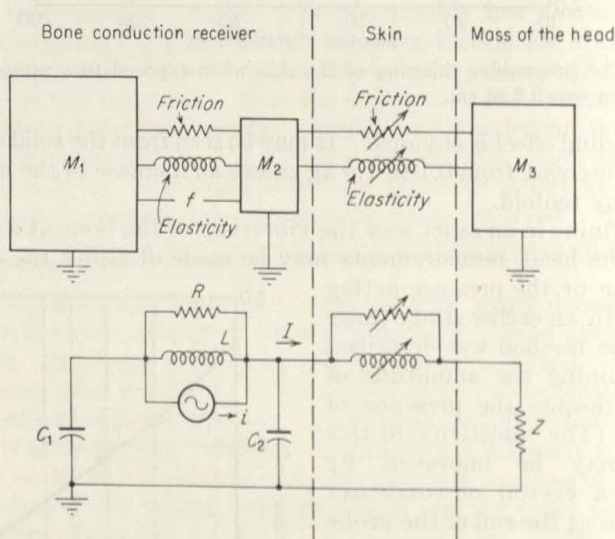


FIG. 6-21. The vibratory system (above) and its electrical analogy (below).

The mass of the head is always exposed to the same pressure as long as the current I flowing through Z remains constant. This condition can be obtained, according to Bárány's observations, by making C_1 very large and tuning the inductance L to resonance with the capacitance C_2 . Then the oscillatory circuit that is parallel to the oscillator has a high impedance, and current i is practically equal to I . Therefore the pressure acting on the vibrating body will be equal to the pressure on the mass of the head. E. Bárány (1) was the first to determine the pressure at the absolute threshold for a bone-conducted tone of 435 cps.

In the use of this method it is necessary with each measurement to tune the bone-conduction receiver to the stimulating frequency. To avoid this tuning the current I or the pressure exerted by the bone-conduction receiver must be measured directly. Then the pressure on the bones of the head is determined also. Here it is assumed that the skin can be represented as a simple elasticity with friction.

Equipment for Pressure Measurements. To measure the pressure acting on the surface of the vibrator a piezoelectric microphone and a condenser microphone were used. In addition to the alternating pressure of a few milligrams there is also a static pressure of as much as 1.5 kg, and a Rochelle salt crystal could not be used on account of its sensitivity to static pressures. A quartz crystal was found to be satisfactory in spite of its low sensitivity.

The arrangement of the quartz microphone is shown in Fig. 6-22. Plates m_1 and m_2 have the same orientation, and their pressure surfaces are provided with metal electrodes. If a pressure P acts upon the cell a voltage V arises between the middle electrode and the two outer electrodes that are connected together, such that

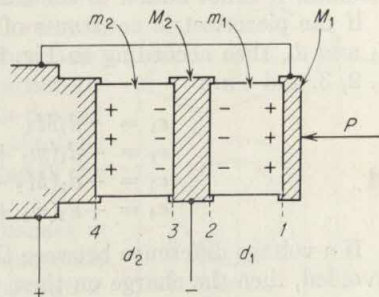


FIG. 6-22. The arrangement of the piezoelectric pressure microphone.

$$V = 2 \frac{d \times P}{C} \quad (6-4)$$

where $d = 6.4 \times 10^{-8}$ cgs is the piezoelectric constant of the quartz and C is the capacity between the two electrodes. The capacity of the connections must be added to C and should be made as small as possible by grounding the two outer electrodes and connecting the middle electrode through a short coaxial cable directly to the grid of an amplifier tube. By this means the wiring capacity can be kept below 5 cm.

This equipment works well, because its operation is independent of frequency and of static pressure effects. It is essential, however, that it be connected to a large mass and that it be kept from moving. If it is fastened to the vibrating end of the bone-conduction receiver, however, the forces set up by the mass of the quartz plates and electrodes will give voltages that are much larger than those produced by the pressure P that is to be measured. These disturbances become greater as the amplitude of motion and the frequency of vibration are increased.

Fahrenheit, Kluge, and Linckh constructed a microphone that was insensitive to over-all movements. However, the mechanical arrangement of the cell described here seemed to fit the purpose of these experiments, and a study was made of the conditions under which it could be made insensitive to movement.

When the cell vibrates along its longitudinal axis, the amplitudes are the same at all points because of the stiffness of the quartz and electrodes. The accelerative forces produced by the vibration therefore are directly proportional to the masses connected to the supporting surface. The pressure on the surface of the cell is zero and increases continuously as the vibrator is approached. If one of the quartz plates is exposed to a

pressure gradient, an electric charge is produced at its electrode surface which is proportional to the pressure. In addition the pressure gradient sets up a space charge inside the quartz, but because quartz is a good insulator it is not added to the charge on the electrode.

If the piezoelectric constants of the quartz plates are represented by d_1 and d_2 , then according to Fig. 6-22 the charges on electrode surfaces 1, 2, 3, and 4 are

$$\begin{aligned} e_1 &= +d_1 M_1 \\ e_2 &= -d_1(m_1 + M_1) \\ e_3 &= -d_2(M_2 + m_1 + M_1) \\ e_4 &= +d_2(m_2 + M_2 + m_1 + M_1) \end{aligned}$$

If a voltage difference between the two plates of the condenser is to be avoided, then the charge on these two plates must be the same, or

$$e_2 + e_3 = e_1 + e_4 \quad (6-5)$$

If the masses of the two quartz plates are made the same so that

$$m_1 = m_2 = m$$

then

$$d_1 = -\frac{3m + 2M_1 + 2M_2}{m + 2M_1} d_2 \quad (6-6)$$

Further, if the mass of the middle electrode is made twice as large as that of the end plates, or $M_2 = 2M_1$, the cell will be insensitive to over-all movements if $d_1 = -3d_2$. This means that charges produced by over-all movements can be avoided if the upper quartz plate is given the usual form and the other plate is reversed in orientation so as to compensate for the charges produced by the first. Because the plate attached to the vibrator is loaded with the greater mass its sensitivity must be made smaller. The sensitivity of the microphone to an externally applied pressure will then be reduced to one-third, but this does not interfere with the measurements.

There are various ways in which the piezoelectric constant of a quartz plate may be reduced. If plane-parallel plates are sawed from a quartz crystal and etched with hydrofluoric acid, it may be observed that particular portions of the plate have exactly opposite orientations from other portions, so that the action of pressures will produce charges of opposite sign. If the plate is cut so that one-third of the surface is opposite in orientation to the remainder, a pressure will produce a charge one-third that of a normal plate. For such a plate to work properly, however, it is essential that the pressure be equally distributed over its entire surface. If this condition is not fulfilled, then it is better to use plates that are uniformly sensitive over the entire surface.

In the quartz crystal represented in Fig. 6-23, the x axis is the electrical axis along which an acting pressure produces the maximum sensitivity. On the other hand, a compression in the z direction, which is known as the optical axis, does not set up any free charge on the pressure surfaces.

Therefore the piezoelectric constant can be made smaller by a relocation of the plane in which the plate is cut. Instead of cutting the plate along the yz plane as indicated for the uppermost disk in this figure, the plane is rotated around the y axis so that the direction of pressure lies in the xz plane and makes an angle δ with the z axis. Then the piezoelectric constant is given by $d_s = d \sin^3 \delta$, when $\delta = 43^\circ 54'$, and the desired threefold reduction of sensitivity is obtained (Voigt). This form of cut is represented in the lower part of Fig. 6-23.

A microphone constructed in this manner is represented in Fig. 6-24. An aluminum tube that could be screwed to the electrodynamic bone-conduction receiver contained an insulating glass tube, and within this tube were the insensitive quartz plate, a brass measuring electrode, a second quartz plate, and an aluminum cover. The masses of the two quartz plates were the same, and the mass of the measuring electrode was twice that of the aluminum cover. The aluminum cover was capped with a piece of aluminum foil that was bound to the end of the tube with thread and served as a shield. This simple construction was satisfactory because in the measurements a static pressure was always present. For many purposes a rubber membrane was stretched over the foil so as to keep the electrodes and quartz plates

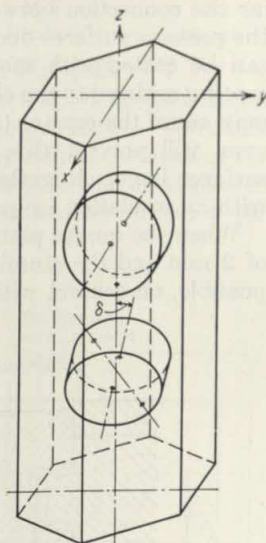


FIG. 6-23. Orientations of the disks cut from the quartz crystal for use in the pressure cells.

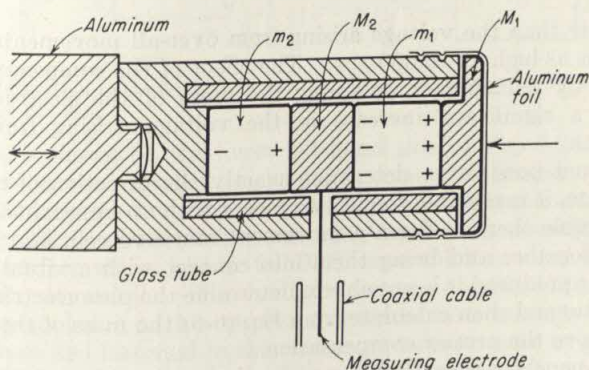


FIG. 6-24. Construction of a pressure cell that is insensitive to gross movements.

pressed together. Also some covers were made with a short tube that could be screwed over the aluminum tube. In order to obtain a suitable degree of springiness the short tube was slit perpendicular to its axis.

At very high frequencies the layer of air between the quartz plate and the electrode may act as a cushion so that for small amplitudes in particular the connection between the two is not stiff enough. If roughing up the pressure surfaces does not solve this difficulty, then the quartz surface can be coated with metal by the cathode-deposition method and this coating soldered to the electrodes. Unfortunately a temperature increase may cause the crystal to crack. [Soldering in a temperature-controlled oven will prevent this.] A metallic connection between the pressure surfaces is not altogether necessary, and the cell can be glued together with an insulating lacquer without impairing its sensitivity.

When the quartz plate was given a diameter of 4 mm and a thickness of 2 mm and the aluminum cover was 7 to 10 mm in diameter, it was possible, on contact with the head, to obtain a voltage that was several

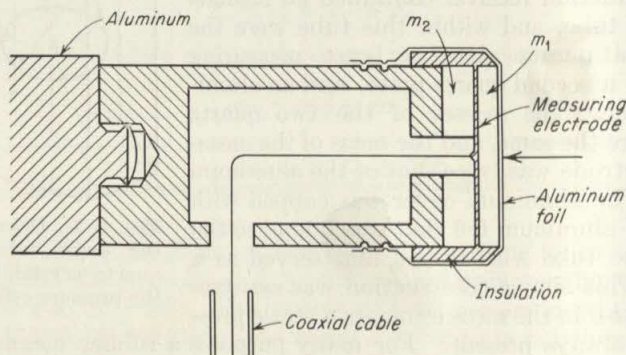


FIG. 6-25. A compensated pressure cell with small mass.

times larger than the voltage arising from over-all movements, even for frequencies as high as 10,000 cps. The effect of the compensation could be tested by reducing or enlarging the mass of the electrodes, which produced a significant increase in the voltage arising from over-all movements.

If it is not possible to determine exactly the direction of cut for the quartz plate, it is possible to cut two pieces with an approximate orientation, assemble them to form a movement-sensitive cell, and then place two cells together and bring them into contact with a vibrator. From the voltage produced it is possible to determine the piezoelectric constants of the plates and then calculate from Eq. (6-6) the mass of the electrodes that will give the proper compensation.

For frequencies above 10,000 cps a further reduction of the disturbance arising from general movements is desirable. This reduction is obtained if aluminum cover M_1 shown in Fig. 6-24 is removed and the upper plate covered only with an aluminum foil, which is pressed directly against the head. If an aluminum foil is also used for the measuring electrode, then according to Eq. (6-5) the instrument is unresponsive to general move-

ments when the two masses of quartz have the relations

$$-\frac{m_2}{m_1} = \frac{d_1}{d_2} + 2$$

A microphone with this construction is shown in Fig. 6-25.

For many measurements it seemed desirable to use a condenser microphone for measurements of static and alternating pressures. To reduce the sensitivity to general movements as much as possible, the mass of the electrodes must be made as small as possible. Therefore an arrangement was used like one reported by Sell (2). A schematic cross section of the

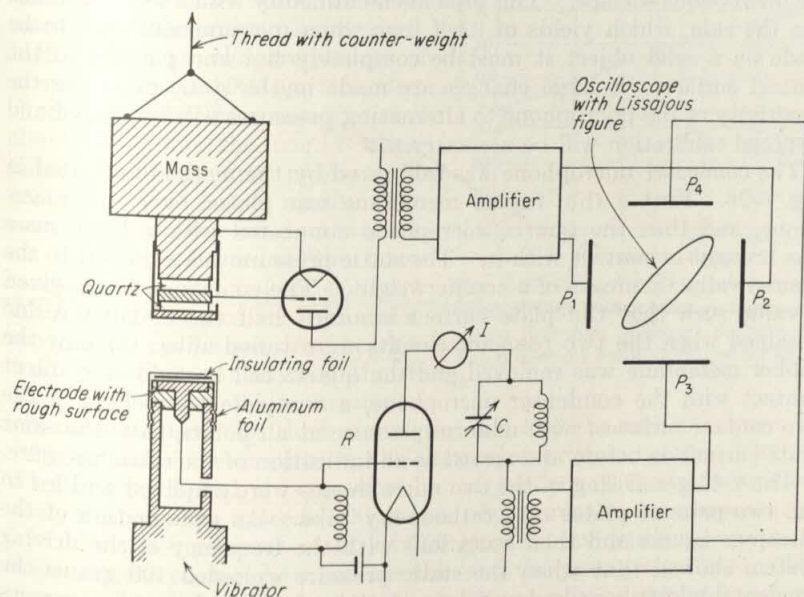


Fig. 6-26. Methods of calibrating the pressure cell and of measuring the transmission of pressure by the skin.

microphone is shown on the lower left-hand side of Fig. 6-26. A short aluminum tube was attached to the electrodynamic vibrator, at the top of which was an insulating ring of plastic. A steel electrode was fastened in this ring, whose plane surface was roughened with a sandblast. On this rough surface was a plastic foil 0.001 mm thick covered in its turn with thin aluminum foil. The aluminum foil was connected to the metal tube and grounded. A thin rubber membrane was strongly stretched over the whole and fastened to the aluminum tube so as to cause the foil to press on the roughened surface. When the microphone had a diameter of 1 cm its capacity was 30 cm, and a pressure of 1 kg increased the capacity to 50 cm.

These changes in capacity were measured by Riegger's half-resonance-curve method. In the circuit shown in Fig. 6-26 the capacity of the microphone, together with an inductance, forms a resonant circuit

between the grid and cathode of the tube R . A similar resonant capacity and inductance are introduced into the anode circuit of the tube. The capacity between grid and anode provides feedback so that the tube comes into oscillation. The plate current varies with the tuning and provides a measure of the capacity of the microphone. The static pressure can be read on milliammeter I , and the alternating pressure after amplification can be observed on an oscilloscope.

An advantage of this condenser microphone is that it is easy to construct and is almost completely unresponsive to general movements. A limitation is that the pressure must always be uniformly distributed over the microphone surface. This presents no difficulty with a soft substance like the skin, which yields of itself, but when measurements are to be made on a solid object it must be completely flat and parallel to the contact surface. If large changes are made in the static pressures the sensitivity of the microphone to alternating pressures will be altered and a special calibration will be necessary.

The condenser microphone was calibrated by the method indicated in Fig. 6-26. First a thin rubber membrane was placed over the microphone, and then the quartz microphone connected with a large mass was brought in contact with it. The static pressure was adjusted to the desired value by means of a counterweight. The condenser C was given a value such that the plate current assumed half the maximal value obtained when the two resonant circuits were tuned alike. If now the rubber membrane was removed and the quartz cell brought into direct contact with the condenser microphone, a complete parallelism of the two contact surfaces, with uniform pressure at all points, gave the same plate current as before and served as an indication of the static pressure.

The voltages arising in the two microphones were amplified and led to the two pairs of plates of a cathode-ray tube. An examination of the Lissajous figures and their variations with the frequency of the driving system showed that when the static pressure exceeded 100 grams the condenser microphone had uniform sensitivity from the lowest frequencies up to 13,000 cps.

Because the quartz microphone was provided with a large mass and therefore exhibited only slight movements, it is possible in this situation to use an uncompensated pressure cell, and the pressure can be determined from Eq. (6-4) if the amplification is known. Also this equipment was used to check the sensitivity as calculated for the compensated microphones.

Sound Transmission through the Skin. The equipment shown in Fig. 6-26 was used to study the nature of sound transmission through the skin and to determine the range of frequencies within which sound pressure is conducted through a layer like the skin of the head without loss of amplitude. For this purpose the web of skin between index finger and thumb was placed between an electrodynamic vibrator and a microphone connected to a large mass.

First to be studied was the effect of static pressure on the transmission. If the vibratory amplitude of the electrodynamic driver was kept constant

and the static pressure was increased, the sound pressure as measured by the upper microphone increased sharply for the low frequencies. Often an increase in static pressure from 100 grams to 1.5 kg gave an increase of as much as a hundredfold. These increases of sound pressure are shown for various frequencies in Fig. 6-27. This effect is well known. When the stem of a tuning fork is placed on the head, the loudness of the bone-conducted tone increases markedly as the pressure is increased.

However, as the frequency of vibration exceeds 3000 cps this effect of static pressure grows smaller, and above 7000 cps the sound transmission is independent of the static pressure. This fact is readily demonstrated with bone-conducted tones, for if the amplitude of the bone-conducted receiver is kept constant the loudness attains its final value above 7000 cps as soon as the skin makes a uniform contact with the vibrator. However, the transmission

still depends upon the thickness of the skin and the area of contact.

If, instead of the amplitude, the alternating pressure produced by the vibrator is measured, it is found to be independent of the static pressure when this pressure exceeds 300 grams. Some results are given in Fig. 6-28. A static pressure of about 300 grams is evidently necessary to ensure a good contact between the skin and the pressure surfaces. The transmission of pressure occurs without loss, as may be proved by taking away the skin so that the microphones are in direct contact with one another. Then the voltage ratio of the two microphones does not change, though the absolute value of the pressure may increase more than a hundredfold.

For static pressures above 0.5 kg and a skin thickness of 2.5 mm it may also be shown that the pressure transmission exhibits variations of only about 2 db for frequencies up to 10,000 cps. A phase shift between the pressures observed on the two sides of the skin becomes noticeable only above 8000 cps. This fact signifies that there are no standing waves in the layer of skin for this range of frequencies.

To investigate this matter further, direct measurements were made of the speed of sound in the skin. The vibrator was made to produce a brief thrust, and the resulting voltage in the microphone was recorded with a dual cathode-ray oscillograph. The time differences found gave a speed of sound above 100 meters per sec for a static pressure of 0.5 kg.

The velocity of sound is probably this large by reason of the fact

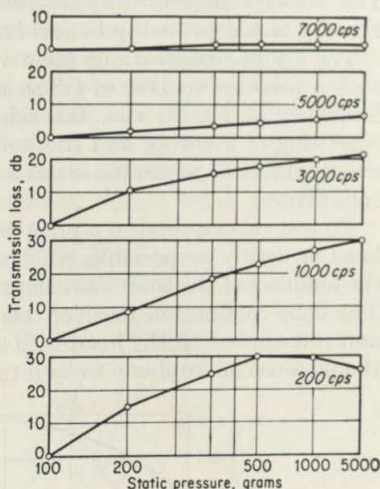


FIG. 6-27. The effects of static pressure on amplitude transmission. Curves are shown for five different frequencies. The skin was 2.5 mm thick and 0.8 sq cm in area.

that the skin, although soft, is thin and adheres to the surface of the vibrator so that it undergoes only a slight degree of lateral displacement. The velocity therefore approaches that of a compression wave. The velocity would probably be less for a thicker layer of skin (Böhme).

The above observations seem to indicate that under the conditions, with a pressure surface of 0.8 sq cm, a skin thickness of 2.5 mm, and a frequency of 10,000 cps, the skin behaves like a transmission system consisting of a spring and friction but without mass. Accordingly, the measurement of pressures seems a satisfactory way of investigating bone conduction.

To test this method in a practical way, the vibrator was applied to the head as lightly as possible, when acting at a frequency of 4000 cps, and the loudness of the tone was compared with that of an air-conducted tone. The bone-conduction receiver then had its amplitude reduced by 12 db, and was applied to the head with sufficient force to restore the reading of the pressure microphone to its former value. The loudness was found to

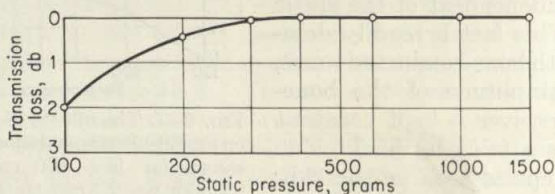


FIG. 6-28. The effects of static pressure on the transmission of vibratory pressures. The vibration had a frequency of 2500 cps, and the skin layer was 2.5 mm thick.

be exactly the same as in the first application. Thus it is proved that the loudness of a bone-conducted tone is represented by the pressure reading and is independent of the properties of the skin.

If the alternating pressure was kept constant, then the loudness of the bone-conducted tone for frequencies up to 2500 cps was the same when the vibrator was pressed directly on the teeth of the upper jaw as when it was applied through the lip, which had a thickness of 6 mm.

Threshold Measurements. The greatest difficulty in the construction of a bone-conduction receiver is in preventing the radiation of aerial waves. The case of the bone-conduction receiver undergoes vibrations whose amplitude is inversely proportional to the ratio between the mass of the case and the mass of the vibrator. The upper surface of the case is usually large, and an audible sound appears even when the vibratory amplitude is small. An attempt was made to reduce this source of disturbance by using two vibrators acting in opposite phase yet symmetrically, so that the case did not vibrate. This arrangement was successful for low and intermediate frequencies, but for the high frequencies it was not possible to avoid a change of phase between the two receivers, especially when the vibrator was applied to the head, so that the symmetry of the two vibrators was lost.

It is possible, however, as Jones and Knudsen found, to reduce the aerial sound by enclosing the receiver in a metal case surrounded with

felt, and having only the vibrating rod exposed to the outside, as shown in Fig. 6-29. Fastened to the outside of the case was a metal ring that held a pair of rubber rings made by cementing the ends of a piece of rubber tubing together. When the vibrator was applied to the head the rubber rings made contact also and formed an airtight juncture. The metal ring was threaded so that it could be adjusted in height, so that the rubber rings would have little effect upon the pressure that the vibrator exerted on the head. The pressure of the rubber ring was so slight as to have no effect on bone conduction. Even pressing on the head with a kilogram weight rarely caused any change, because the skin is highly elastic.

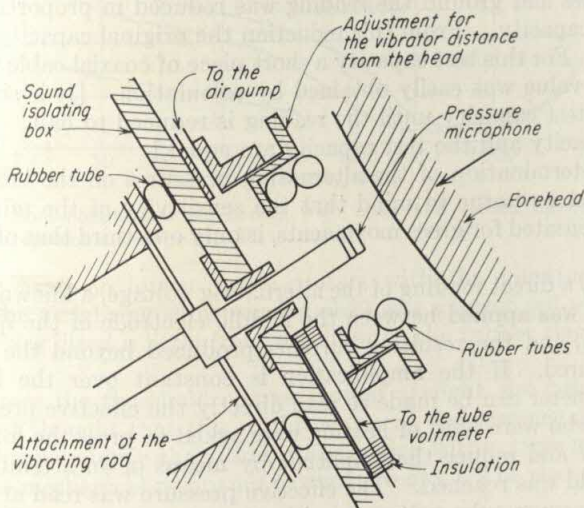


FIG. 6-29. Construction of a pressure bone-conduction receiver with low emission of aerial sound.

The bone-conduction receiver was supported at an angle so that when the head was bent forward a contact was made with the forehead. The contact pressure then consisted simply of the head's own weight. Any lateral slipping of the head was prevented by the large contact surface of the rubber ring. For some of the more protracted observations it was found better, in order to maintain the contact pressure and keep the head position steady, to introduce a suction into the cavity enclosed by the ring.

For precise measurements it is important to keep the static pressure within close limits, for though there is no change in the transmission through the skin there may be a small variation in the conduction from the frontal bone to the ear. The pressure on the head can alter the elastic properties of the bony wall.

The vibrator consisted of an aluminum tube extending all the way through an electrodynamic system with membranes at the two ends to hold it parallel. The two membranes were made as stiff as possible so that the amplitude of vibration would not be changed by the loading of

the head. Otherwise it will be found that when contact with the head is removed the amplitude rises sharply, and the forces of inertia in the quartz microphone become so large, especially for high frequencies, as to produce a false indication caused by the over-all movement. It is not possible to make the microphone sufficiently insensitive to gross movements under these conditions.

The quartz microphone shown in Fig. 6-24 was used for most of the measurements. The capacity of the instrument was measured by placing a small mass on its surface and setting it into vibration so that a particular reading was obtained. Then if a known capacity was introduced between the electrodes and ground the reading was reduced in proportion to the increase in capacity. From this reduction the original capacity could be calculated. For this test capacity a short piece of coaxial cable was used, because its value was easily obtained by calculation. [It is simplest to adjust this test capacity until the reading is reduced to half. Then the original capacity and the test capacity are equal.]

In the determination of the alternating pressures on the basis of Eq. (6-4) it must be borne in mind that the sensitivity of the microphone, when compensated for gross movements, is only one-third that of ordinary quartz.

To obtain a direct reading of the alternating voltage, a known alternating current was applied between the middle electrode of the quartz cell and ground, and the resulting currents produced beyond the amplifier were measured. If the amplification is constant over the frequency range, the meter can be made to read directly the effective pressure.

Persons who were hard of hearing were asked to press the forehead on the vibrator and reduce the amplitude by means of an attenuator until the threshold was reached. The effective pressure was read at the same time on a vacuum-tube voltmeter with a logarithmic scale. For persons with normal hearing, however, the amplification often was insufficient to give a reading. It was not possible to increase the amplification because of inadequacy of shielding. Therefore, after the threshold was reached, the head was held as still as possible and the amplitude of the vibrator was increased tenfold or a hundredfold by pressing a button. This procedure was possible because for vibrations of this magnitude the response of the system was linear.

The threshold measurements were made on the middle of the forehead because at this place they are most reproducible. On the side of the head the sensitivity is about 10 db greater, but the values may change by this amount when the vibrator is shifted a few millimeters.

The thresholds for various frequencies and with the meatus open and closed are given in Fig. 6-30. For the latter series the entrance of the meatus was closed airtight by means of a very light rubber membrane. It appears that closure of the meatus increases the loudness for tones up to about 2000 cps. This increase in loudness was also measured directly. The ear was closed with a finger, and at the same time an attenuator was adjusted so that the loudness was the same as with the ear open. The necessary change in attenuation is shown in Fig. 6-31. Beyond 200 cps

there are sometimes large increases in loudness, but these are usually limited to narrow bands of frequency. Sometimes also closing the ear with a finger produces a reduction of loudness. If the vibrator is placed on the side of the head the increases of loudness are usually larger. In these tests care was taken to keep the loudness at a high enough level so that there was no disturbance from the humming tone produced by the finger. A further precaution was to make sure that no sound was audible

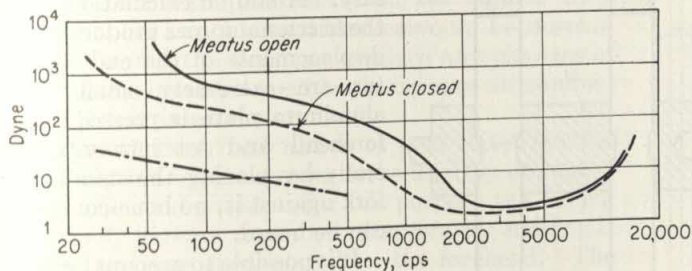


FIG. 6-30. Bone-conduction thresholds with open and closed meatus. The dot-dashed line represents a slope of 0.77.

when the head no longer made contact with the vibrator. For this purpose the metal ring shown in Fig. 6-29 was screwed out so that when the head was lifted a little from the vibrator the rubber rings still made contact.

Sometimes the threshold curves showed a slight rise below 500 cps. It was first thought that this might be due to the presence of overtones. To test this possibility the vibrator was loaded with a large mass so as to reduce the mechanical resonance to about 70 cps. The mass acted like a

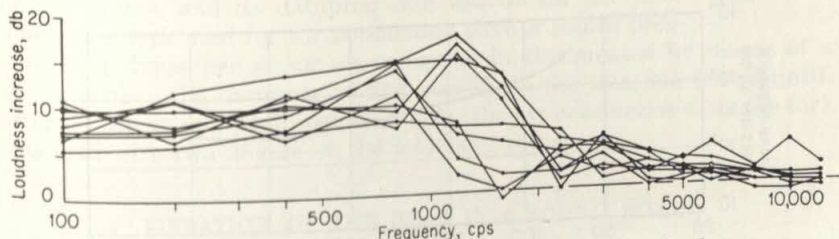


FIG. 6-31. Effects on loudness of closing the meatus with the finger.

filter, yet the measurements of threshold were the same as before. However, these observations were not well reproducible, because it was continually necessary to adjust the resonance as the static pressure of the head changed. To avoid this a mechanical low-pass filter was constructed. It consisted of four loudspeaker diaphragms, two brass rings, and three brass cylinders assembled as in Fig. 6-32. With this arrangement it is easily possible to reduce the first overtone about 35 db more than the fundamental. Here also the static pressure results in a change in the tuning to the fundamental frequency, because it stretches the

loudspeaker diaphragm and changes its elasticity. However, this does not disturb the measurements. The values obtained from the thresholds were exactly the same as before.

This filter has the disadvantage of being subject to lateral vibrations. Such vibrations can be avoided by the use of restraints as suggested by

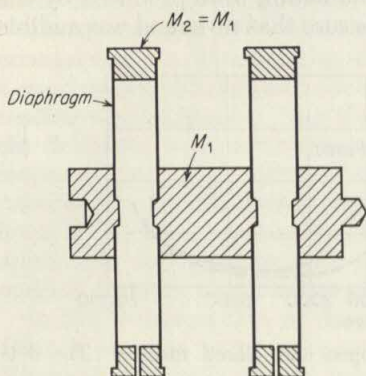


FIG. 6-32. A mechanical low-pass filter. The middle cylinder M_1 connects the second and third diaphragms.

Gerdien (see Müller-Pouillet, 1), but in the present situation they are not necessary. A simple calculation shows that the frictional forces produced by lateral displacements of the end of the vibrator are extremely small. If a flat aluminum plate is pressed against the forehead and set into vibration laterally by placing the stem of a tuning fork against it, no bone-conducted tone can be heard.

It is possible to account for the change in threshold sensitivity produced in the low frequencies by a closure of the meatus. Thus if the frontal bone is caused to vibrate at low frequencies the whole mass of the skull executes parallel displacements. Only the lower jaw remains relatively motionless because of its inertia, since it is not directly connected with the other bones. The meatus is compressed, because it is close to the articulation of the jaw (see page 144). Then when the meatus is closed there arises a variation of air pressure that acts upon the eardrum.

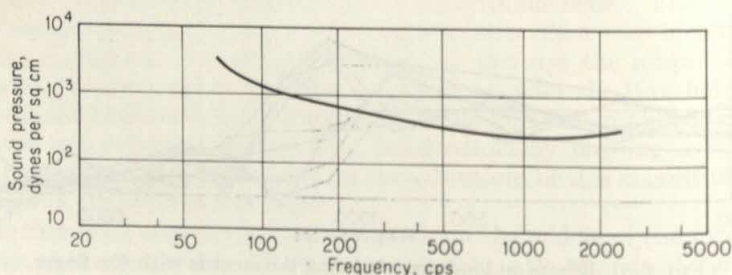


FIG. 6-33. Threshold curves in a person after radical mastoid operations on both ears.

When a constant pressure acts on the mass of the head, the resulting amplitude of vibration varies inversely as the square of the frequency, *i.e.*, as n^{-2} , when n is the frequency. Therefore the pressure variations in the auditory meatus decrease as n^{-2} . It is known that for low tones the sensitivity of the ear by air conduction increases with frequency almost exactly as $n^{2.77}$. But because the sound pressure in the meatus becomes less as the frequency rises, the increase in sensitivity by bone conduction only increases as $n^{0.77}$. This function is represented in Fig. 6-30 by the

dot-dashed line, which has nearly the same slope as the threshold curve in the region of 50 to 500 cps.

The prominent increase in sensitivity in the region of 2000 cps apparently is associated with a resonance of the ossicles. It disappears after a radical mastoid operation, in which the eardrum, malleus, and incus are removed. Figure 6-33 shows the mean threshold obtained in a person after this operation had been performed on both ears, and in whom the clinical tests indicated the inner ear and auditory nerve to be normal. A closure of the meatus does not produce any changes of loudness after this operation, evidently because air conduction on such a ear is extremely weak.

The equipment described above is well suited to the absolute calibration of the tuning forks used by otologists for tests of bone conduction. For this purpose the tuning fork was usually given a maximal vibration, by striking it on the knee, and was then placed on the forehead. The tone that was heard was compared in loudness with the tone of a bone-conduction receiver whose characteristics were known. It is also possible to fasten a pressure microphone of small mass directly to the tuning fork and place the fork on the forehead. The sound pressure generated by the fork is then read directly.

Most otologists use a 256-cps fork for testing bone conduction. Ordinarily it is provided with a broad base as shown in Fig. 6-34. Such a fork, with a total length of 18 cm, when maximally excited gave a force by bone conduction of 5×10^5 dynes when applied with a static pressure of 500 grams, and its damping rate was 57 db per min. The same fork used for air conduction gave a sound pressure of 4 dynes per sq cm as measured in the meatus by means of a sound probe. Its damping at first was 35 db per min and fell off until, after 30 sec, it was 22 db per min. For the air-conduction tests the fork was held with two fingers at the middle of the stem.

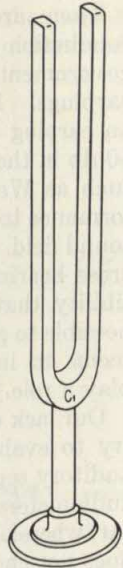


FIG. 6-34. A tuning fork for bone-conduction tests.

VIBRATION OF THE HEAD IN A SOUND FIELD*

Routine audiometric measurements have shown that it is difficult to measure the thresholds of hearing of both ears if the difference between the two thresholds is more than 40 db. In this case "cross hearing" (Lane)—hearing with one ear the tone that is delivered to the other, which is usually attributed to bone conduction through the head—makes it necessary to mask the more sensitive ear. The intensity of the masking noise must be adjusted for each listener so that the threshold of the ear to be measured is not changed. Many persons are disturbed by the unfamiliar noise.

* Article 52 as listed in the Author's Bibliography. Published in 1948.

The purpose of the following investigation was to find a way to reduce cross hearing and thereby make it possible to dispense with the masking noise. With this aim, measurements were made of the amplitude of the vibrations of the skull, using several types of receivers in order to find out which type produced the smallest effect.

There are many other problems in which the relation between air conduction and bone conduction plays a role. During the war many governments spent considerable sums of money for the development of earplugs. In these developments, it was found impossible to construct an earplug whose attenuation for air-borne sound was more than 35 to 40 db in the frequency range between 100 and 8000 cps. Some authors, such as Watson and Knudsen, have attributed this limitation of performance to the vibrations set up directly in the bones of the head by the sound field. Inasmuch as the amount of insulation is about the same for cross hearing and for earplugs, it is interesting to investigate the possibility that the mechanisms are also the same. (The fact that it is possible to get greater attenuation than 40 db in an ear filled with earwax seems to indicate that factors other than bone conduction may also play a role.)

Our lack of knowledge on this point is particularly disturbing when we try to evaluate the effect of a surgical operation aimed at improving auditory sensitivity. For instance, after an otosclerosis operation some audiometers show improvement of the nonoperated as well as the operated ear, whereas with other audiometers the threshold of the nonoperated ear does not change.

So far as the writer is aware there exists only one monograph dealing extensively with hearing by bone conduction, namely, the paper by E. Bárány in 1938, though many of the problems were perceived by duVerney more than two centuries earlier.

Vibrations of the Skull. When the skull touches a vibrating body, the vibrations are transferred to the skull. If the frequency of the vibrations is low, we can expect the whole skull to vibrate as a rigid body. If we assume the neck to be soft in comparison with the skull, we may expect the movements of the head to be translational movements. At higher frequencies, the forces caused by the inertia of the head enter the picture, and the skull undergoes deformations. As a result nodal lines appear on its surface. The frequency at which the change in the vibratory pattern occurs is important in the study of bone conduction.

It is difficult to measure the vibrations of the bony wall with a pickup because soft skin is an inefficient transducer of the vibrations of the bony wall. The thickness of the skin, furthermore, changes from one place on the head to another, so that it is necessary to develop a method of measurement that is independent of the properties of the skin.

The impulse method was used to measure the elastic and frictional constants of the skin of the forehead. A vibration pickup with a round surface 30 mm in diameter was pressed against the forehead with a pressure of 3 kg. (This is the most convenient pressure because it does not fatigue the neck muscles and can easily be produced by the arm,

making it possible to hold the pickup in the hand.) When the incisors were clicked together, the bones of the head were given an impulsive movement, and the pickup was set momentarily into oscillation. Oscillograms showed that when the mass of the pickup was multiplied by four, the frequency of the damped oscillations was halved. But for a further increase of the mass this rule did not hold, because the mass of the pickup was no longer small in comparison with the mass of the head.

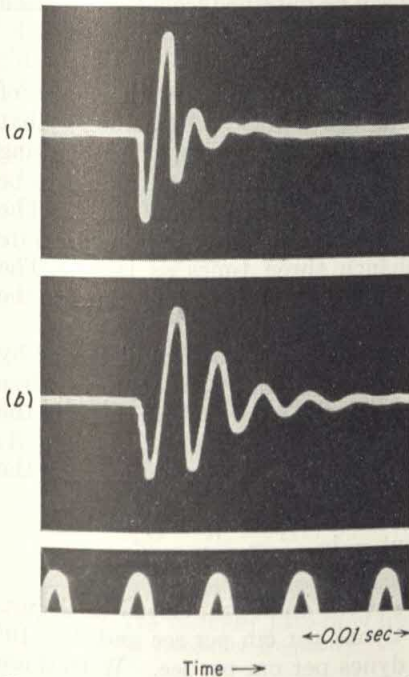


FIG. 6-35. Damped oscillations recorded by a pickup. The stimulus was a clicking of the teeth. The mass of the pickup was 230 grams for *a* and 460 grams for *b*.

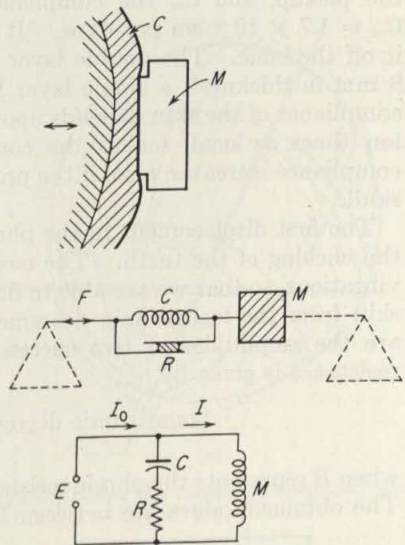


FIG. 6-36. The pickup system with its mechanical and electrical analogies.

A layer of rubber between the skin and the pickup diminished the frequency of the oscillations of the system consisting of the skin and pickup together.

The upper photograph of Fig. 6-35 shows the damped oscillations of a pickup on the forehead when the pickup was given a mass m of 230 grams and a pressure surface 30 mm in diameter. The lower photograph was made under the same conditions but with a mass m of 460 grams. The time marks occur at intervals of $\frac{1}{100}$ sec. The 3-kg pressure on the pickup was maintained by a very flexible spring, so that a small change in the position of the supported end of the spring did not modify the oscillations.

These oscillations indicate that the skin pickup system can be represented by the analogous electrical circuit shown by Fig. 6-36 (see Fire-

stone, 1). The mechanical resistance across the skin is due to the radial flow of the skin under the pressure surface during the vibrations. The clicking of the incisors is represented in the electrical analogy by a short voltage pulse in the resonant circuit. The velocity amplitude of the vibration is given by the current through the mechanical or electrical elements.

The compliance, *i.e.*, the displacement under unit force, of a patch of skin of the forehead (area $S = 7$ sq cm) can be obtained from the equation

$$f = 1/2\pi(mC_m)^{1/2}$$

where f is the frequency of the damped vibrations, m the mass of the pickup, and C_m the compliance of the skin. It was found that $C_m = 1.7 \times 10^{-9}$ cm per dyne. It is possible to fold the skin by lifting it off the bone. The double layer of skin thus formed was found to be 8 mm in thickness, a single layer being presumably 4 mm thick. The compliance of the skin depends upon the pressure. Making the pressure ten times as small makes the compliance three times as large. The compliance increases, also, if the pressure is applied for a long time to the skull.

The first displacement in the photographs of Fig. 6-35 is distorted by the clicking of the teeth. The next vibrations, however, represent free vibrations, so that we are able to determine the frictional constant of the skin from the logarithmic decrement of the vibrations. If A_1 and A_2 are the amplitudes of two successive vibrations, the equation for the resistance is given by

$$\text{Logarithmic decrement} = \ln \frac{A_1}{A_2} = \frac{R}{2mf}$$

when R represents the ohmic resistance in the analogous electrical circuit. The obtained values are between 10^5 dynes per cm per sec and 3×10^6

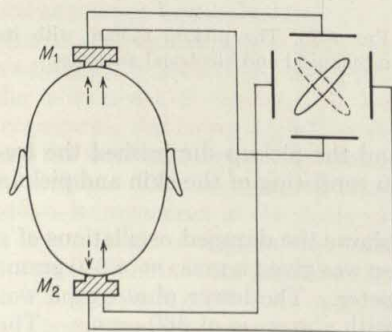


FIG. 6-37. Determination of the resonance frequency of the head by phase observations.

dynes per cm per sec. With these values, it is possible to calculate the transmission of the skin pickup system. Bárány measured the mechanical properties of the skin by a different method, using a smaller knob. His result for the compliance is about the same as the present in so far as it is possible to make a comparison.

The best way to investigate the vibratory pattern of the skull seemed to be to measure the phase of the vibrations at different places on the skull. From the phase pattern it is possible to see what part of the bony wall is moving inward and what part outward. The setup for the phase measurement is shown in Fig. 6-37. The microphone M_1 on the forehead is con-

nected to the vertical plates of a cathode-ray tube. The microphone M_2 on the back of the head is connected to the horizontal plates of the tube. For low frequencies the movements of various parts of the head are simple parallel movements in the same direction. The vibrations as recorded by the two microphones are opposite in phase, and on the screen of the cathode-ray tube we see a trace like the continuous line in the figure. Upon raising the frequency to 1000 cps, we find that the line remains in this position. As we go beyond 1000 cps, however, the trace becomes vertical, and around 1500 cps it reaches the position of the dotted line. At this frequency the forehead moves forward as the back of the head moves backward, and vice versa.

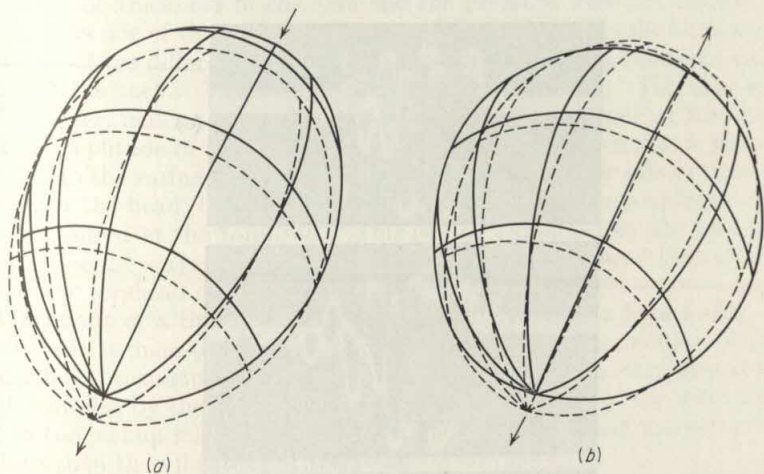


FIG. 6-38. The vibratory pattern of the skull (a) below the resonance frequency and (b) above the resonance frequency.

For these observations it is necessary to measure the phase of the vibrations of the bone as transmitted through the skin. Because the thickness of the skin varies from place to place, valid measurements are possible only if a method can be found that is not influenced by the mechanical properties of the skin. It is well known that for a resonant circuit, like the skin pickup system, the phase between the force and velocity of the pickup approaches a constant value as the frequency is increased beyond resonance. To measure the phase, therefore, it is necessary only to keep the frequency well above the resonance frequency of the system.

A bone-conduction receiver was placed on the forehead, and one of the pickups was placed nearby. The other pickup was pressed against the back of the head. Up to the frequency of 1500 cps, the vibrations of the skull of a male subject were translational movements, as shown in Fig. 6-38a. At 1600 cps the back of the head showed no movement; only the forehead vibrated. At 1800 cps the vibrations of the back of the head were about as large as the vibrations of the forehead. This longitudinal

compression and expansion of the skull marked the first resonance frequency. A further rise in frequency moved the nodes of the vibratory pattern to the forehead until once again the back of the head did not vibrate. At a still higher frequency a new node was formed and moved again toward the forehead. These observations are in agreement with earlier measurements (see page 130).

From the fact that the resonance frequency of the skull is 1800 cps we have to conclude that the wave velocity of the deformation along the surface of the skull cannot be high. As shown in Fig. 6-38*b*, the movements of the forehead and the back of the head are, at 1800 cps, just in phase relative to the surface of the skull. Therefore the wavelength of

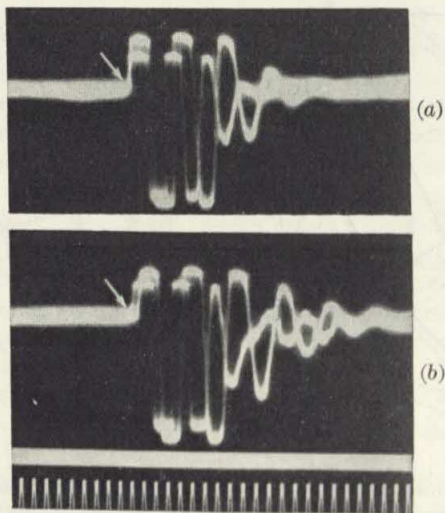


FIG. 6-39. Measurements of the wave velocity along the skull wall. In (a) two pickups were on the forehead, and in (b) one was on the forehead and the other on the back of the head. The source of vibration was a clicking of the incisors.

the skull deformation is equal to one-half the circumference of the head—30 cm in the present case. This gives a phase wave velocity c of 540 meters per sec for 1800 cps.

A direct determination was made of the wave velocity of the deformation by pressing one pickup on the forehead and a second pickup on the back of the head and measuring the difference between the times of arrival of a wave caused by a clicking of the incisors. The deformation produced by this click propagates over the whole skull, one wave going over the crown of the head and another along the base to the back of the head. The thickness of the bony wall is much greater at the crown of the head than it is at the base. Considering only the starting points of the waves in the oscillograms of Fig. 6-39, we are therefore measuring the velocity of propagation at (or in the vicinity of) the crown of the head, because the velocity is higher in the thicker wall.

The oscillograms were made with a dual-beam cathode-ray oscillograph with a common time base. The two vibrations were clipped at different amplitudes so that it would be possible to refer each trace to its proper pickup. To counterbalance inequalities in the pickups, four pictures were taken: (1) with the two pickups on the forehead, (2) with the first pickup on the forehead and the second on the back of the head, (3) with the two pickups on the back of the head, and (4) with the first pickup on the back of the head and the second on the forehead.

Record *a* of Fig. 6-39 shows the two pickups together on the forehead. There is no time difference between the starting points of the two waves. The frequency of the oscillations was different for the two pickups, because the thickness of the skin and the pressure were not exactly the same. As one of the pickups was moved past the ear to the back of the head, the time difference increased progressively until it reached a maximum at the back. This is represented in *b* of Fig. 6-39. The time scale is $\frac{1}{1000}$ sec, making the wave velocity $c = 570$ meters per sec for clicks.

The amplitude of the component of the traveling wave that is perpendicular to the surface decreases as we pass around either side or over the crown of the head, but at the back it again reaches the amplitude that was measured at the forehead. This can be explained by the fact that the size of the wavefront is larger on the sides of the head than it is at either the forehead or the occiput.

Vibrations of a Sphere and of the Human Head in a Free Field. It is difficult to measure the vibrations of the head that occur in a free sound field because a pickup is activated not only by the vibrations of the skull but also by the air-borne sound. The vibrations of the wires leading to the pickup may indeed transfer a greater amount of motion to the pickup than the vibration of the skull.

Fortunately, Lichte succeeded in calculating the forces acting on a sphere, and the calculation was extended to a pulse wave by Zoller. If R is the radius of the sphere, p the sound pressure in a free field, λ the wavelength, f the frequency of the sound, F the force acting on the sphere, m the mass of the sphere, and A the displacement amplitude, we have the following equations:

$$F = 4\pi R^2 p \left[\frac{\lambda}{2\pi R} \cos \frac{2\pi R}{\lambda} - \left(\frac{\lambda}{2\pi R} \right)^2 \sin \frac{2\pi R}{\lambda} \right] \quad (6-7)$$

$$A = \frac{F}{m(2\pi f)^2}$$

A man who weighs 64 kg has a head that weighs about 4.5 kg, according to H. Vierordt. If we take for the average radius of the head $R = 9$ cm and the sound pressure in the free field $p = 10^3$ dynes per sq cm, we obtain for the elongations of this sphere at various frequencies the values shown by the heavy solid curve of Fig. 6-40. The short-dashed curve represents the vibratory amplitude of a plane disk with the same mass $m = 4.5$ kg and the same pressure surface, when the sound pressure acted only on one side of the disk. At frequencies near 1000 cps, the movements of the

sphere are larger than the movements of the disk because at this frequency the diameter of the sphere is about the same as the half wavelength of the sound; the pressure acts in the same direction on both sides of the sphere. As the wavelength becomes small relative to the diameter of the sphere, the amplitude of vibration of the sphere drops rapidly.

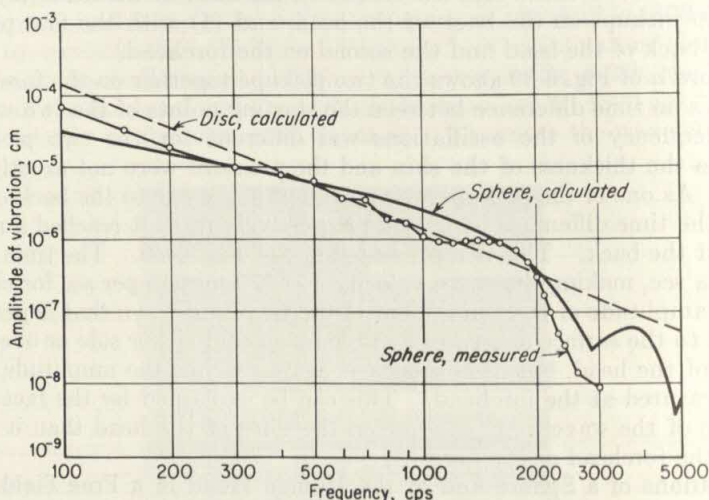


FIG. 6-40. The vibratory amplitudes produced in a sphere or a disk in a free sound field. The heavy solid curve represents calculated values for a sphere, the long-dashed curve represents calculated values for a disk, and the thin curve with dots represents measured values for a sphere.

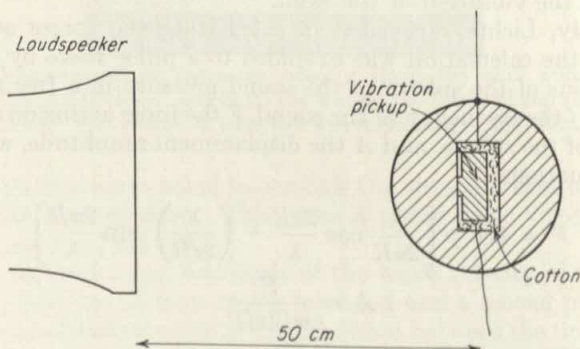


FIG. 6-41. Wooden sphere with a pickup fixed in the center.

For measuring the vibrations, a wooden sphere was used with the pickup fixed in the center. The two halves of the sphere were screwed together as shown in Fig. 6-41, and all seams were filled with plasticine. The distance between the sphere and the loudspeaker was about 50 cm. This distance was large enough to make it possible to neglect the distortions caused by the nature of the wavefront. The thin curve of Fig.

6-40 shows some measurements made with a commercial vibration pickup. The agreement between the measurements and the calculated values is fair if we take into consideration the difficulties of measurement. A sphere of larger radius and greater mass, when the pickup was placed in different orientations with respect to the direction of the sound, also yielded measurements in good agreement with the calculations. It is difficult and expensive to build a vibration table for the calibration of a pickup, particularly at high frequencies. It is easy, however, to make precise measurements of sound pressure. It appears, therefore, that the measurement of the vibrations of a sphere in a sound field provides a convenient method for the calibration of vibration pickups. For this purpose the pickup is put in a small sphere made of plasticine, so that sound waves within the sphere will not disturb the measurements.

In the situation considered, the pickup was surrounded by the wall of the sphere, and air-borne sound waves did not disturb the measurements. But the vibratory amplitudes of the head can be measured only by placing the pickup in contact with a peripheral part of the head, *e.g.*, the teeth. The pickup is thus exposed to the sound field and must at the same time have as small a mass as possible, so that it can follow the vibrations of the teeth.

When the radius of the sphere is small relative to the wavelength λ of the sound, we obtain for Eq. (6-7)

$$F = \frac{1}{3} \times 4\pi R^2 p \frac{2\pi R}{\lambda}$$

and for the amplitude of the motion

$$A = \frac{F}{(2\pi f)^2 m} = \frac{p}{2\pi f \rho c} \quad (6-8)$$

Here ρ is the average density of the sphere and c is the sound velocity. The amplitude of vibration of a small sphere is independent of the radius of the sphere and inversely proportional to the frequency. A comparison with the wooden sphere, as a substitute for the head, shows that up to 1000 cps a small pickup with a density $\rho = 1.5$ grams per cu cm has the same amplitude of vibration as does the head which we wish to measure. Above 1000 cps the vibrations of the small pickup in the free sound field are larger than those of the head.

If we need a pickup that vibrates with so small an amplitude that, when we bring it into contact with the head, the amplitude is increased at least three times (which is suitable for our purposes), we must use a pickup with density $\rho = 4.5$. Changing the shape of the pickup is of little avail. There are, however, some places on the sphere at which, because of interference, the sound pressure at high frequencies is smaller than it is in the free field. It may therefore be possible to measure the vibrations of the wooden sphere at the minimum points.

The pickup used here was a small cylinder 2 cm in diameter and 2 cm in

length. In its center was a pendulum, as shown in Fig. 6-42. When a vibrating body is brought into contact with it, the housing of the pickup

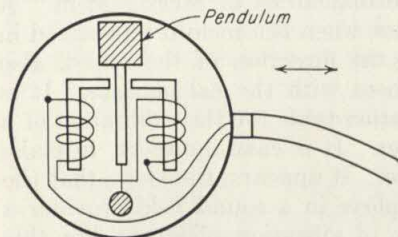


FIG. 6-42. Electromagnetic pickup with high sensitivity for vibrations and low sensitivity for air-borne sounds.

makes the same movement as does the vibrating body, and the bob of the pendulum stands still. The relative movements were recorded electromagnetically. To assure high sensitivity over the entire frequency range under investigation, three pickups were used with different resonance frequencies. In this way it was possible also to eliminate the disturbing movements of the muscles of the head and hand.

To measure the vibrations of the head the calibrated wooden sphere was located about 50 cm from the head in a sound field. The sound pressure was adjusted so that the pickup touching the sphere gave a fixed output; then it was changed until the pickup touching the teeth yielded the same output. From the difference between the two sound pressures, it was possible to calculate the amplitude of vibration of the teeth. Below 1000 cps the measurements were easily reproducible: no differences were found between the amplitudes of vibration of different teeth of the upper jaw. Near 1200 cps there were some resonances in the cavity of the mouth, so that the opening of the mouth could change the amplitude of vibration. At 2400 cps the incisors showed resonance frequencies and had amplitudes of vibration four times as high as the molars. The amplitudes of the lower jaw were always about one-third of the amplitude of the upper jaw. The measurements were made with sound pressures between 30 and 100 dynes per sq cm. Figure 6-43 shows the measured amplitudes extrapolated for a sound pressure $p = 10^3$ dynes per sq cm. The vibrations are definitely larger than those of the corresponding wooden sphere. The vibrations of the head correspond to those of a wooden sphere with a mass between 3 and 3.5 kg. The effective mass of the head is therefore smaller than the static mass.

Relative Amplitudes of Vibration of the Air Particles, Eardrum, Stapes, and Basilar Membrane. To provide a better picture of the relative importance of head movements in response to a sound pressure of $p = 10^3$ dynes per sq cm, the lowermost curve of Fig. 6-43 shows the absolute threshold for hearing by bone conduction as measured at the forehead. These are the smallest amplitudes of vibration of the forehead that can be detected by the ear. The auditory meatus was open, and the measurements were made by the method previously described (page 51), which gives measurements of the vibrations of the bony wall through the skin.

For purposes of comparison, a calculation was made of displacement amplitudes A of the air particles in a free sound field for a sound pressure $p = 10^3$ dynes per sq cm. If ρ is the density of air, c the velocity of the sound in air, and f its frequency, we have again $A = p/2\pi f\rho c$. This

result is based upon practically the same assumptions as those underlying Eq. (6-8). The eardrum can reach this sensitivity only by resonance. Even if the eardrum had no weight, so that it could follow exactly the vibrations of the air, we still would not have at the lower frequencies the same amplitudes of vibration that exist in the free field. The volume V of the middle-ear cavity is about 2 cu cm. If a cavity of this volume were closed with a weightless drum of surface area $s' = 0.66$ sq cm, the displacement amplitude of the imaginary eardrum (see page 137) would be $A = Vp/\rho c^2 s'$.

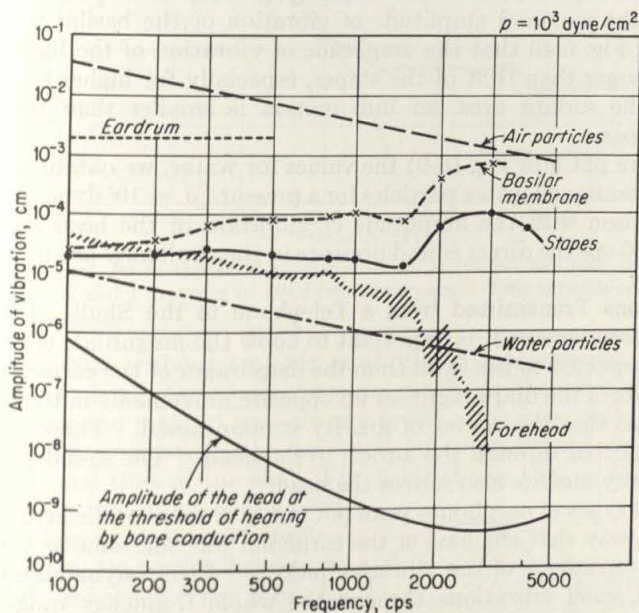


FIG. 6-43. Upper six curves, amplitudes of vibration of the human head, eardrum, stapes, basilar membrane, and air and water particles for a sound pressure of 10^3 dynes per sq cm. Lowermost curve, amplitude of the head at the threshold of hearing by bone conduction.

The real eardrum does not make pistonlike translational movements but turns about an axis on its upper edge. If the middle of the drum is observed, the movements seen at low frequencies are about the same as the movements calculated from the volume elasticity (page 70). This means that the vibrations of the eardrum are limited not by the elasticity of the eardrum but by the elasticity of the air volume. The amplitude of this type of vibration is independent of the driving frequency (the driving pressure being held constant). The vibrations of the eardrum are equal in amplitude to those of the air particles in the free sound field at frequencies around 1000 cps. Above this frequency so many resonances influence the movement of the eardrum that the transmission is highly irregular.

It is possible to determine the amplitude of vibration of the stapes for a sound pressure $p = 10^3$ dynes per sq cm in the following manner. First, we determine the pressure transformation in the ear canal (see Wiener and Ross, and page 268) so that we have the ratio between the pressure on the eardrum and the free sound field. From the pressure on the eardrum we calculate the volume displacement of the round window (page 432). If we assume that the volume displacement of the round window is the same as that of the stapes, we obtain the amplitude of vibration of the middle part of the stapes as shown in Fig. 6-43. Measurements of the volume displacement of the stapes (page 455) make possible a calculation of the maximal amplitude of vibration of the basilar membrane. We see in Fig. 6-43 that the amplitude of vibration of the basilar membrane is larger than that of the stapes, especially for higher frequencies, because the surface area set into motion is smaller than the surface of the stapes.

When we put into Eq. (6-9) the values for water, we obtain the amplitude of vibration of water particles for a pressure $p = 10^3$ dynes per sq cm. A comparison with the amplitude of vibration of the head shows that above 2500 cps the direct sound pressure in the skull may be an important factor.

Vibrations Transmitted from a Telephone to the Skull. For audiometric measurements it is important to know the magnitude of the vibrations transmitted to the skull from the diaphragm of the earphone. The movements of the diaphragm set up opposite movements in the earphone housing, so that the center of gravity is maintained. These vibrations are transmitted through the auricle to the head. The sound pressure in the auditory meatus also moves the head.

Several types of earphones were put one at a time on the artificial head in such a way that the axis of the earphone was the same as the axis of maximal sensitivity of the vibration pickup. Electrodynamic earphones produced small vibrations through the whole frequency range. Most magnetic earphones, on the other hand, had very bad resonances. Rubber earphone cushions greatly reduced the vibrations at low frequencies. When two earphones were placed on the head and connected in such a way that their diaphragms vibrated symmetrically, the amplitude of vibration of the head at high frequencies was only a few decibels below the value produced by one earphone.

The same measurements were made on the actual head, and the vibrations of the molars in the direction of the phone were determined with the small pickup. Figure 6-44 shows the amplitudes of vibration for a sound pressure $p = 10^3$ dynes per sq cm at the eardrum. The solid curve shows the values for a dynamic earphone and the broken curve those for a magnetic earphone. Each earphone had a rubber cushion (type MX-41/AR).

Cross Hearing. When only one ear is partially deafened, it is difficult to obtain an exact threshold for the deafened ear. The sensitive ear hears the tone transmitted through or around the head from the deafened ear. The transmission loss from one side of the head to the other side,

for dynamic earphones with rubber cushions, is 40 to 50 db in the frequency range from 100 to 10,000 cps (Lane). It is possible to make threshold measurements on the deafened ear only by using a masking noise in the better ear. The intensity of the masking noise must be adjusted in each individual case. Because the masking noise tends to

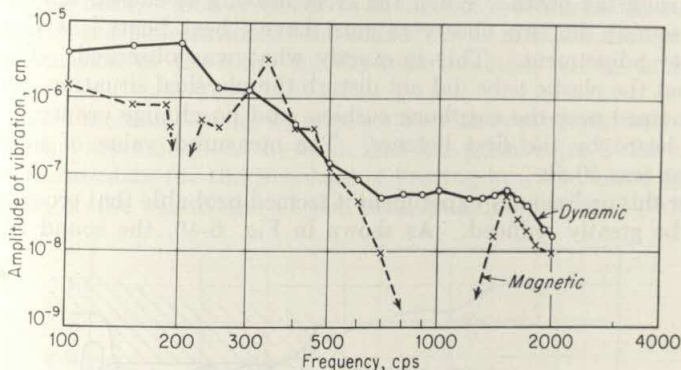


FIG. 6-44. Vibrations of the skull produced by an earphone mounted on one side of the head, for a sound pressure of 10^3 dynes per sq cm. Two types of earphone were used, as indicated.

disturb patients without training in threshold measurements, it seems important to have, for some cases, an earphone that would minimize cross hearing and make it unnecessary to use a masking noise.

A comparison between the amplitude of vibration of the eardrum (Fig. 6-43) and that of the skull (Fig. 6-44) shows that at 1000 cps, for example, the vibrations of the head are 90 db lower. It seems improbable, therefore, that cross hearing in the middle frequency range is due to skull vibrations.

Sound vibrations can pass from one ear to the other by following the band of the headset or by traveling around the head. Measurements showed that at low frequencies a difficulty arose as a result of transmission by way of the headband when certain magnetic earphones were used. In those instances, it was sufficient to isolate the earphone case from the band of the headset by a piece of rubber, as shown in Fig. 6-45. With most of the earphones, however, the headband was not an important leakage path.

In order to examine the possibility of the cross hearing of air-borne sound, a small plastic tube was introduced through the rubber cushion (MX-41/AR) of the right earphone (Fig. 6-45), and this tube was con-

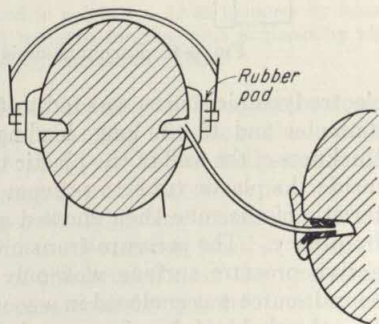


FIG. 6-45. Experiment showing that cross hearing is due to air conduction and not to bone conduction.

nected to the ear of a second subject. Then the second subject could hear the tone in the ear canal of the first subject. In the first subject's left ear there was a strong tone of frequency $f_1 - 1$ cps so that a beat of 1 cps was heard. By Lane's method, the sound pressure on the right side was adjusted in such a way that the sound intensity went through zero during the beats. When the cross hearing is caused only by airborne sounds the two observers must have "best beats" at the same intensity adjustment. This is exactly what was observed. To make sure that the plastic tube did not disturb the physical situation, the tube was clamped near the earphone cushion, and no change occurred in the sound heard by the first listener. The measured value of interaural isolation was 50 db.

After this preliminary experiment it seemed probable that cross hearing could be greatly reduced. As shown in Fig. 6-46, the sound from an

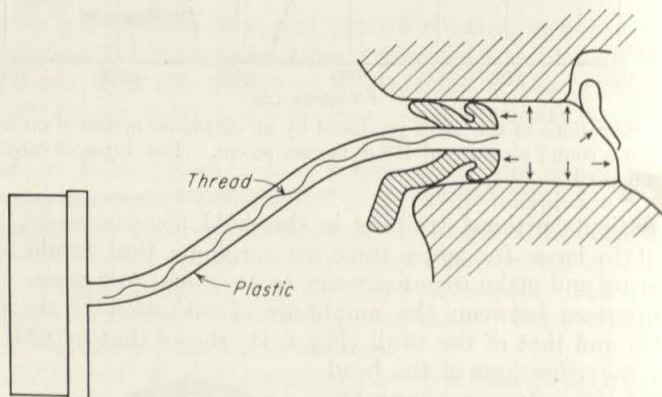


FIG. 6-46. Earphone designed to minimize cross hearing.

electrodynamic source was fed to the ear through a plastic tube 3 mm in diameter and 15 cm long, leading through a perforated earplug. The thickness of the wall of the plastic tube was 0.3 mm. A thread was placed inside the plastic tube to prevent resonance. The transmission characteristic of the tube then showed a fairly smooth decline with increasing frequency. The pressure transmitted to the head was small because the active pressure surface was only the cross section of the tube. The sound source was enclosed in a soundproof box. When a tone 5 db above the threshold of hearing was led to the opposite ear, it usually was necessary to increase the pressure in the tube almost to the threshold of feeling to obtain a beat that went through zero loudness. This appears to indicate that the plastic tube and earplug combination permits little cross hearing.

Even when an ordinary earphone is used to test uniaural hearing, it is possible to reduce cross hearing by using an earplug in the other ear. The reduction of the cross hearing is approximately equal to the sound insulation provided by the earplug.

Hearing by Bone Conduction in a Free Sound Field. The problems of hearing despite middle-ear deafness, and hearing despite the use of ear-plugs, make it important to know to what extent air-borne sound can be heard by bone conduction. The impact of the sound waves on the head leads to three different kinds of bone conduction: (1) the direct movement of the whole head, which gives rise to an inertial reaction on the auditory ossicles, (2) the penetration of the sound waves into the head, and (3) the deformation of the skull by the mass reaction acting during the vibrations.

If we assume that hearing by bone conduction is produced only by the translational movements of the head, then it is possible (as E. Bárány has shown) to calculate for the threshold of hearing in a free sound field the amplitude of the vibrations of the head, and to compare it with the

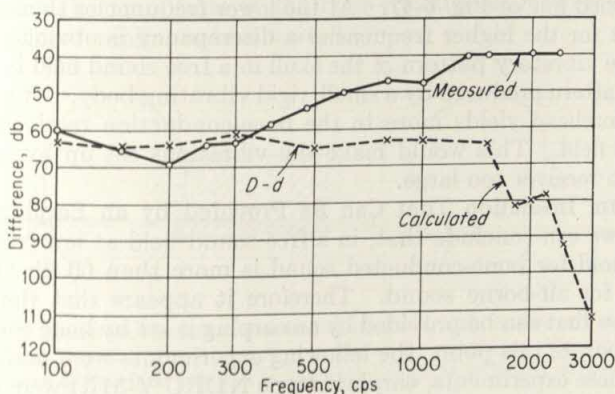


FIG. 6-47. Intensity of the sound field required to produce a given loudness by bone conduction, expressed in decibels above that required for the same loudness by air conduction. The two curves show calculated and measured values.

amplitude of vibration at the threshold of hearing by bone conduction. These calculations lead to the conclusion that the vibrations that reach the cochlea by bone conduction are 48 to 53 db below the pressure of the air-borne sound in the frequency range from 200 to 800 cps.

We have seen that the skull changes its vibratory pattern at high frequencies. It is necessary, therefore, to determine whether at high frequencies the amplitude of vibration of the head, *i.e.*, of the forehead, alone is important, or whether we must also consider the deformation of the skull.

To investigate this problem, the following experiment was performed. First, a bone-conduction receiver was placed on the forehead and adjusted in amplitude of vibration until a pickup, also on the forehead, gave an easily measurable voltage. Then the sound pressure of the free field was adjusted until the loudness of the air-borne sound was the same as that of the bone-conducted sound. Finally, with the head moved away from the bone-conduction receiver, the sound pressure was raised until the pickup yielded the same output that it had done in response to the

bone-conducted vibrations. The ratio between the two sound pressures, expressed in decibels, is represented by the smooth curve in Fig. 6-47. In these measurements, the transmission characteristics of the skin and fatigue of the ear do not play any role.

Figure 6-43 shows the amplitude of vibration of the forehead in a sound field with a pressure of 10^3 dynes per sq cm and also the amplitude of vibration of the forehead at the threshold of hearing. The differences d between these two curves can be expressed as decibels above threshold. With the aid of standard curves* we can also determine the difference in decibels between the pressure $p = 10^3$ dynes per sq cm and the threshold pressure for aerial sounds. If we call this difference D , then $D - d$ represents the number of decibels by which air-borne sound is more effective than bone-conducted sound. The calculated values are shown by the dashed line of Fig. 6-47. At the lower frequencies the agreement is fair, but for the higher frequencies a discrepancy is obvious. Above 400 cps the vibratory pattern of the skull in a free sound field is different from the pattern produced by a small, rigid vibrating body. It is possible that the forehead yields more to the bone-conduction receiver than to the sound field. This would make the vibrations set up by the bone-conduction receiver too large.

Maximum Insulation That Can Be Provided by an Earplug. From Fig. 6-47 we can conclude that, in a free sound field at low frequencies, the threshold for bone-conducted sound is more than 60 db above the threshold for air-borne sound. Therefore it appears that the limit of attenuation that can be provided by an earplug is set by bone conduction. To demonstrate this point, the following experiments were performed.

In all these experiments, earplugs (type NDRC V-51R) were used and were pressed so deep into the auditory meatus that the attenuation was more than 40 db at all the frequencies tested. The fact that it is possible, at 200 cps, to improve the attenuation from the ordinary value of 35 db to a value of 45 db by pressing the earplug deep into the meatus makes it appear probable that the limit for the attenuation is set by the meatus. That there is no relationship between the skull vibrations and the attenuation shows that the attenuation is the same in the free sound field as it is when the sound is delivered through an earphone, even though the measured amplitudes of vibration are different.

Watson and Knudsen found that it was impossible to produce a further improvement by covering the pinna with a steel shield. This fact was easily confirmed. But because it seemed possible that the pressure on the steel plates was transmitted to the meatus by the cartilaginous tissue, two open tubes 25 cm long and 7.5 cm wide, filled with cotton, were used. When these two tubes were pressed against the sides of the head as shown in Fig. 6-48, an attenuation of 62 db was obtained in a 200-cps free field.

The inverse experiment was performed by having a listener, with earplugs in his ears, bite on a rod on the end of which there was a disk. Even when the surface of the disk was twice as great as the surface of the head (500 sq cm), biting on the rod did not make the sound louder. With

* See *J. Acoust. Soc. Amer.*, 1936, 8, 143.

a surface area of 5000 sq cm, however, the listener did hear a difference, at 200 cps, when he effectively enlarged his head by biting on the rod.

We may deduce from Fig. 6-47 that the pattern of the vibration of the skull is the same for the sound field as for the bone-conduction receiver for low frequencies. With a bone-conduction receiver, therefore, an attempt was made to cancel the low-frequency bone vibration set up by the sound field.

For this purpose a sound was caused to impinge normally upon the forehead, and at the same time the amplitude and phase of the vibrations of a bone-conduction receiver on the forehead were adjusted in such a way that a pickup showed no movements of the forehead. With an earplug providing 40 db of attenuation it was not possible to obtain any change in the loudness by switching the bone-conduction receiver on and off. Only by increasing the amplitude of the bone-conduction receiver by 25 db could a loudness minimum be obtained.

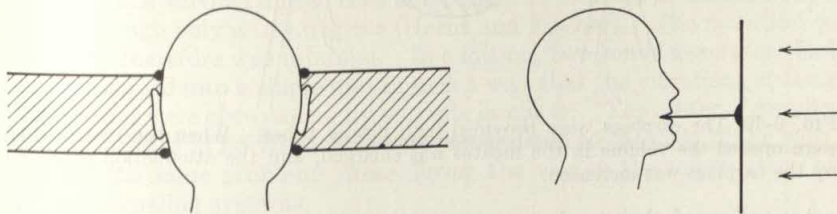


FIG. 6-48. The sketch on the left shows two tubes filled with cotton and placed firmly over the ears to improve the attenuation produced by earplugs. The sketch on the right shows how the surface exposed to the sound may be enlarged without changing the isolation of the ears.

From all these experiments we must conclude that the maximal attenuation that earplugs can provide is determined by the attenuation in the external meatus. Watson and Knudsen found that the attenuation provided by the same earplug in a metal block was about 60 db and concluded that the softness of the skin limits the attenuation of an earplug. In fact, it is well known from the otosclerosis operation how easy it is to lift the skin and the eardrum from the wall of the meatus.

The movements of an earplug can be transmitted to the eardrum in two ways: (1) by a movement of the skin in the meatus and (2) by sound pressure in the meatus. To investigate the first possibility a small vibrating ring was put into the meatus so as barely to touch the skin. By adjusting the position of the ring it was possible to make the vibrations sound very weak. When the meatus of the opposite ear was closed, the tone appeared to shift to the other side. This indicated that the tone was heard by bone conduction. Therefore the movement of the skin in the canal can be neglected.

In the second case, the movements of the earplug produce a sound pressure in the meatus which is inversely proportional to the volume of the meatal cavity. Therefore, if the cavity is made larger, the attenua-

tion provided by the earplug must be increased. Figure 6-49 shows the setup. Through the perforated earplugs, tubes of plastic 40 cm long, 3 mm in diameter, 0.3 mm in wall thickness, and 2.8 cu cm in volume were introduced into the two ears. The distal ends of the tubes were closed. When the two tubes were clamped near the ear canal, the

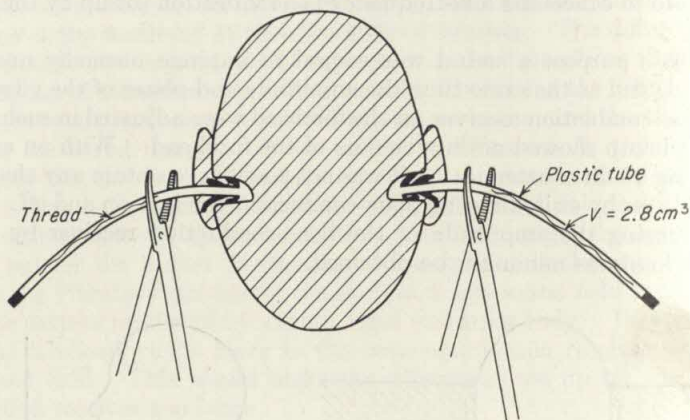


FIG. 6-49. The earplugs were provided with plastic tubes. When the two clamps were opened the volume in the meatus was enlarged, and the attenuation provided by the earplugs was increased.

attenuation of the earplugs was 40 db for 200 cps. When the clamps were opened the attenuation was increased by about 6 db. By putting a thread in the tubes it was shown that resonance phenomena did not play any role.

In the frequency range from 20 to 3000 cps, many earplugs produced almost constant attenuation, with changes of only a few decibels. It

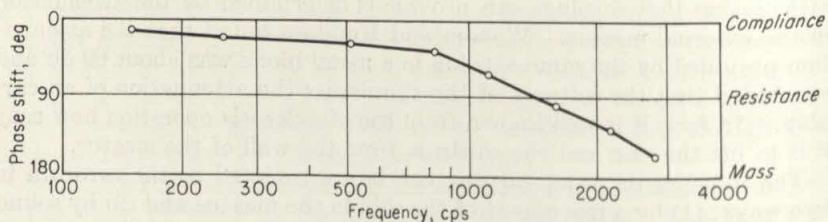


FIG. 6-50. The phase shift produced by an earplug in the meatus.

would be easy to explain this fact if the forces acting on the earplug could be shown to be pure elastic forces. For this purpose measurements were made of the phase of the vibrations of the earplug. The driving force was a thermal noise of a half-octave band width. (It is possible to obtain a half-octave band width by using two commercial octave filters staggered by half an octave.) With the aid of a resistance-capacitance phase shifter, the receivers on the two ears were adjusted to provide the same loudness, and they were set in such a phase relation that the image of the

noise appeared in the middle of the head. Then one ear was closed with the earplug, the loudness balance was readjusted, and the phase shift necessary to place the image of the sound again in the middle of the head was measured. Because the earplug changed the volume into which the earphone operated, the volume under the earphone without the earplug was reduced by putting some plasticine in the space between the earphone and the eardrum. The phase shift introduced by the earplug is shown in Fig. 6-50.

STRUCTURE OF THE MIDDLE EAR AND HEARING OF THE VOICE BY BONE CONDUCTION*

A number of years ago during a visit to a ship, the writer was much impressed by the fact that the fog signal, which was heard for many miles at sea, was practically inaudible in the cabin of the ship. To produce this effect a large number of similar sound generators had been mounted in a vertical line so that the sound was radiated in the horizontal plane through only a few degrees (Hecht and Fischer). The radiation to the cabin therefore was minimal. In addition, two sound generators had been combined into a single unit in such a way that the vibrations of their diaphragms were always exactly opposite in phase. The center of gravity did not move, and no vibrations were transmitted to the body of the ship. Exactly the same problems arose during the war in the construction of air-raid signaling systems.

It is well known that the construction of the middle ear is very complicated, as shown in Fig. 2-1. It is difficult to understand why the transmission of the vibrations from the air to the fluid of the cochlea requires three ossicles of peculiar form. It would seem that many purposes must be served besides the transmission of vibrations from the air to the cochlea.

It is well known from fossil impressions in stone that in prehistoric times the higher types of living creatures consisted only of fishes and insects. In the subsequent evolution of reptiles, frogs, mammals, and birds, it is possible to follow the development of the ossicles from the gills of the fishes (Broom). It is assumed that this development was governed by the principle of fitness. It was important for an animal that his voice be heard as far as possible and at the same time that his ear be sensitive to sounds coming from the outside. The following section reviews the physical characteristics of the middle ear through which auditory sensitivity was increased for sounds coming from the outside and decreased for sounds produced by the organism itself. In this relation, E. Bárány (1) has already pointed out that the malleus is provided with a head in order to minimize the rotations of the ossicles during hearing by bone conduction.

Sensitivity of the Ear of Lower Animals to Their Own Vocalizations.
It is to be expected that for lower animals the manner of reduction of the

* Article 53 as listed in the Author's Bibliography. Published in 1949.

ear's sensitivity to the animal's own vocalizations will take a simple form. For instance, frogs produce intense sounds with a frequency range comparable to that of mammals. In Fig. 6-51 the frog investigated (*Rana pipiens*) is shown with his large eardrum to the right of the photograph. The elastic properties of the membrane are similar to the properties of the eardrum of a calf. When the frog croaks, he opens his mouth and vibrates the end of his tongue. These vibrations subject the eardrum, lying at the surface of the skull, to intense sound pressures. But these sound pressures are compensated for from the other side of the membrane



Fig. 6-51. Head of a frog, showing the eardrum.

because the Eustachian tube of the frog is very wide. As shown in Fig. 6-52, it is possible to see about half of the eardrum through the Eustachian tube when the mouth of the frog is open. Consequently, because the sound pressure acts on both sides of the drum simultaneously, the net vibration is minimized. Figures 6-51 and 6-52 show that the distance of the eardrum from the corner of the mouth is so small that the compensation can be correct in phase and amplitude even for relatively high frequencies. It is a peculiar fact that by opening his mouth the frog enlarges his Eustachian tube in the ratio of about 1:2. The structures surrounding the opening in the frog and in man are similar, and the Eustachian tube of a man, which is usually closed, is also opened by a wide opening of the mouth (for instance, when a person yawns).

There is another method of reducing the hearing of one's own voice by air conduction. This method, used by the rooster, consists of closing the external meatus. This animal was investigated because by crowing it also is able to produce large sound pressures. When the feathers are cut away the opening of the meatus can be seen (Fig. 6-53a). This opening in the skin is surrounded by a cartilaginous ring which can easily be pulled in such a way that the opening of the meatus is narrowed or closed, as shown in Fig. 6-53b. A closing of the meatus results from a movement of the cartilaginous ring similar to that produced in raising

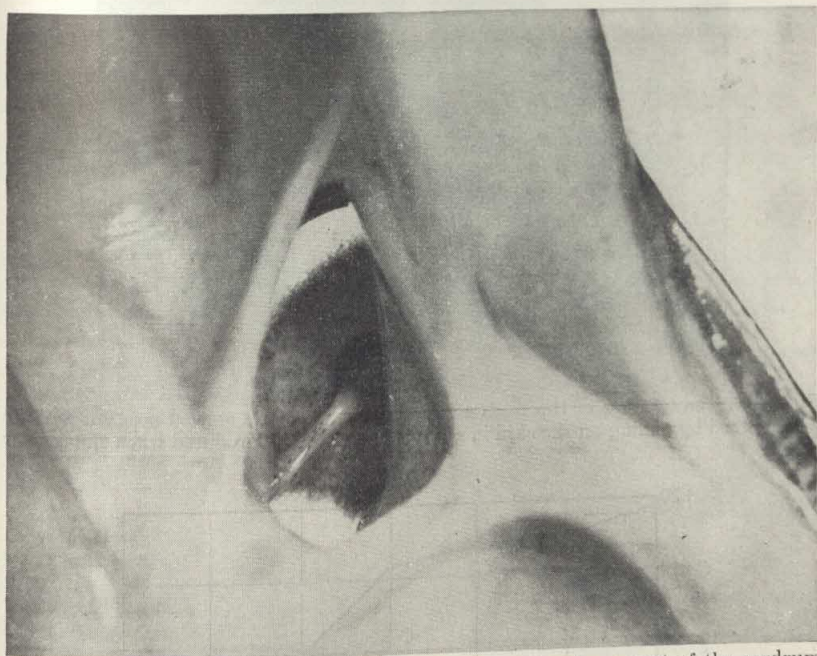


FIG. 6-52. A view from the mouth cavity of a frog, showing a part of the eardrum through the opening of the Eustachian tube. The ossicle is seen fixed to the middle of the drum.

the head when the rooster crows. This simple arrangement reduces the sensitivity of the ear during vocalization.

The adjustments that minimize the sensitivity of the mammalian ear during phonation are more complicated than the ones employed by the frog and rooster.

Air and Bone Conduction for the Hearing of One's Own Voice. To find out something about the radiation of sound during vocalization, the sound pressure was measured near the mouth and the head. A condenser microphone with a small metal tube in front of the diaphragm was used. The intensity of the vocalization was maintained at a constant value with a second microphone, and at the same time measurements were made of the changes in sound pressure at different places near the mouth and

around the head. Figure 6-54 shows how the average intensity of speech varies along the front-to-back axis of the mouth. It was necessary to choose as a reference point a position 1 cm in front of the lips in repose, in order that movements of the lips during speech would not interfere with

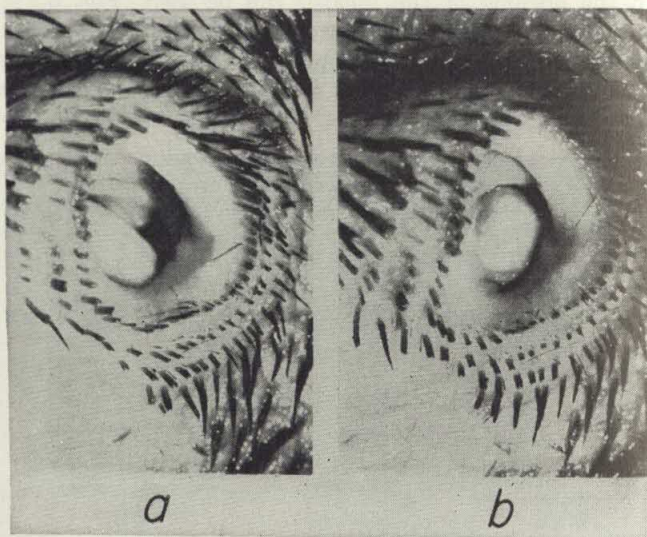


FIG. 6-53. The opening of the meatus of a rooster (*a*) in its normal position and (*b*) when closed by pulling on the skin in a way similar to that produced when the rooster crows.

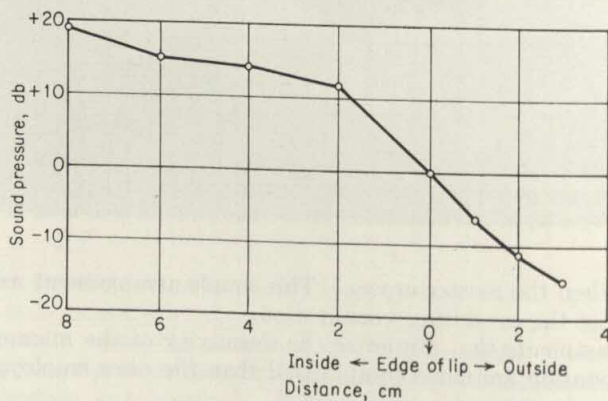


FIG. 6-54. Average sound pressure, at different points inside and outside the mouth, produced by vocalization.

the microphone tube. The average intensity increase from the lips to the inside of the mouth was found to be about 15 db. Outside the mouth the intensity falls off rapidly; the drop from the lips to the opening of the ear canal is about 20 to 25 db, when all types of vocalizations are averaged. This attenuation changes somewhat with frequency, and in Fig. 6-55

the attenuation for different frequencies is shown. In these measurements a series of narrow bandpass filters were used.

Curves of equal sound pressure in the horizontal plane near the mouth are shown in Fig. 6-56 for one speaker. The curves on the left side

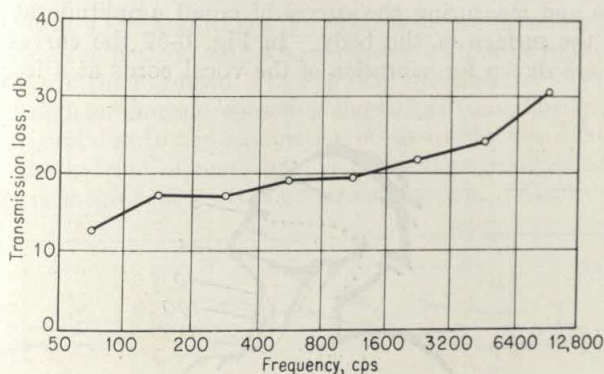


FIG. 6-55. Average transmission loss between the brim of the lips and the opening of the meatus, for twelve different vowels. The measurements were made for octave bands, and the points represent the mid-frequencies of the bands.

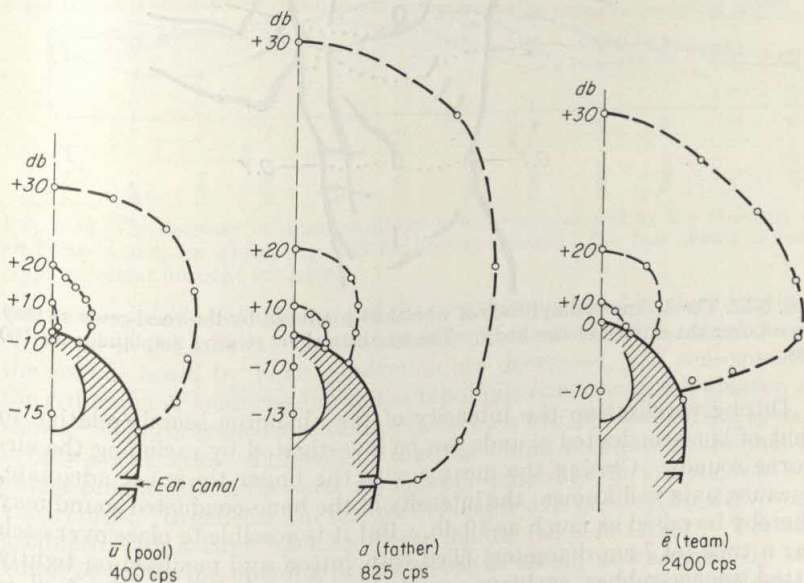


FIG. 6-56. Contours of equal sound pressure around the mouth for the vowels $\bar{o}\bar{o}$, $\bar{a}$, and $\bar{e}$, measured on one subject.

represent the sound pressure for the lower formant of the vowel $\bar{o}\bar{o}$ ($\bar{p}\bar{o}\bar{o}l$) with a frequency of about 400 cps. The point midway between the outer edges of the open lips was taken as the reference point for sound pressure. The middle figure shows the curves of equal sound pressure for the lower

formant of the vowel *ā* (fāther), and the curves to the right represent the high formant for the vowel *ē* (tēam) with a frequency of about 2400 cps.

The vibrations from the vocal cords are distributed over the whole body. It is possible to estimate the damping of these waves by using a stethoscope and measuring the curves of equal amplitude at an angle normal to the surface of the body. In Fig. 6-57 the curves of equal amplitude are shown for vibration of the vocal cords at a frequency of 100 cps.

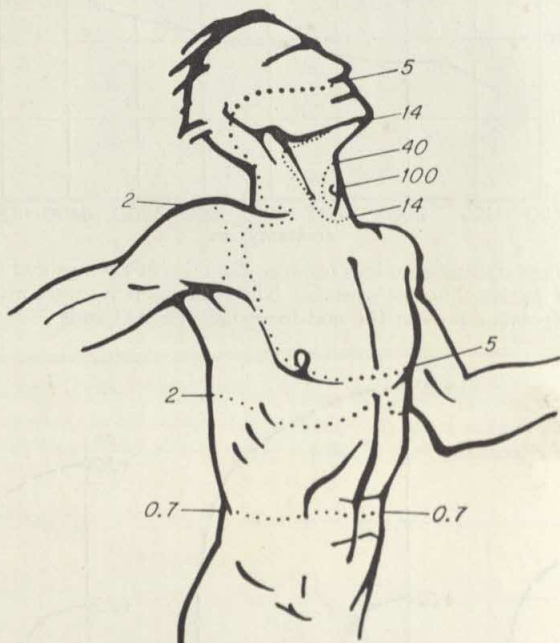


FIG. 6-57. The decline in amplitude of vibrations produced by the vocal cords as they travel over the surface of the body. The numbers show relative amplitudes for 100 cps.

During vocalization the intensity of the air-borne sounds relative to that of bone-conducted sounds can be investigated by excluding the air-borne sounds. Closing the meatus with the finger tip is not adequate, because, as is well known, the intensity of the bone-conducted sound may thereby be raised as much as 10 db. But it is possible to place over each ear a tube (of 7-cm diameter) filled with cotton and mounted on tightly fitted sponge-rubber cushions, so that an airtight fit to the skull is obtained. By testing with a bone-conduction receiver on the forehead it can be shown that the addition of the two tubes has not changed the loudness of the bone-conducted sound for any frequencies. In putting the tubes on the ears it is important that the tubes be placed as high as possible so that the lower edge of the pinna is in contact with the tube, because when the tube is too low, parts of the vibrating neck muscles are

enclosed in the tube cavity and can produce air-borne sounds to actuate the eardrum. The sound isolation for air-borne sound with the cotton-filled tubes in place was about 30 db in the frequency range from 150 to 4000 cps.

When the tubes were placed on the ears, the speaker heard his own vocalizations at a lowered intensity. This decrease in loudness could be measured by a comparison with a bone-conducted tone of 1000 cps applied to the middle of the forehead. In Fig. 6-58 this decrease in loudness for whispering and for normal speech is shown for four different subjects. The attenuation due to the elimination of air conduction is about 6 db. Therefore the hearing of one's own voice by bone conduction is of the same order of magnitude as it is by air conduction. When we whisper,

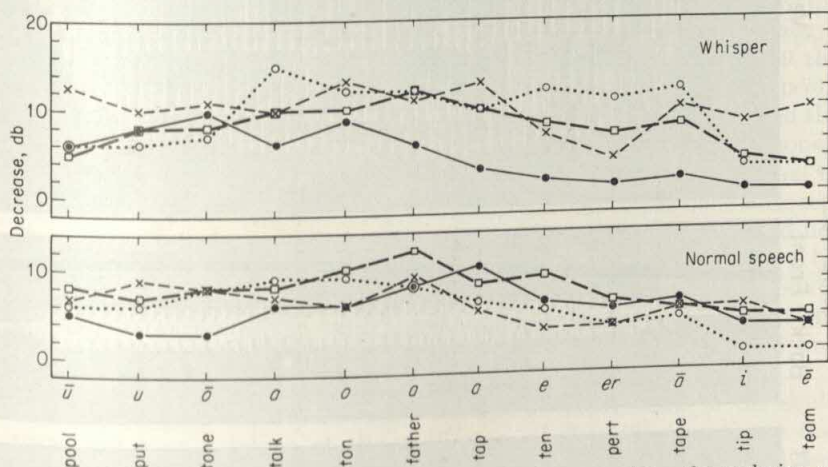


FIG. 6-58. The decrease in loudness of one's own voice caused by the exclusion of air-borne sound, for whispering and for normal speech. The four curves in each graph represent different subjects.

the vocal cords do not vibrate and the sound is produced by the vibrations of the air in the mouth. In the absence of vibrations of the vocal cords, the sounds heard by bone conduction are decreased, and consequently the reduction in loudness due to the tubes put over the ears is greater, as shown. The difference in intensity between a whisper and normal speech is only about 5 db. This means that the sound pressures in the mouth cavity produce about the same amount of loudness as the vibrations of the vocal cords. In general, the decrease of loudness is greatest for the vowels produced with a large opening of the mouth (as *ā* in *fāther*). For the vowel *ōō* (*pōōl*) the opening of the mouth is small, and accordingly the sharpness of resonance is great and there is a large pressure difference between the inside of the mouth and the mouth opening. The relatively high sound pressure in the mouth increases the vibrations of the lower jaw, and therefore the sound *ōō* is heard as rather loud by bone conduction.

Vibrations of the Skull during Vocalization. The tongue of the frog vibrates in the direction of the longitudinal axis of his body. Con-

sequently, the frog's vocalization sets his whole body into longitudinal vibration. Considerable progress in decreasing the vibrations of the body is made when, as in mammals, there are two vocal cords rather than one, and these two vibrate symmetrically in a lateral direction. Then the

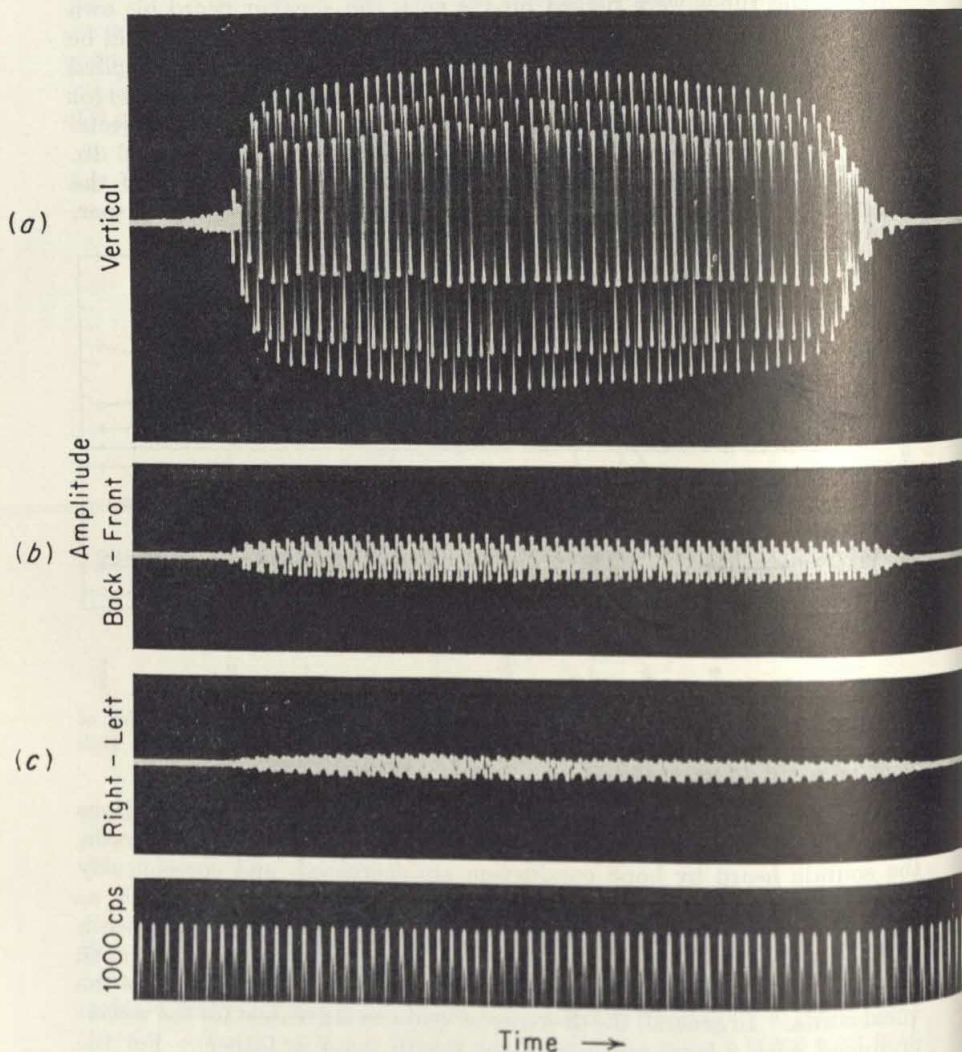


FIG. 6-59. Measurement of the three orthogonal components of the vibrations of the skull during phonation of the vowel *oo* as in *pool*.

center of gravity of the vocal organ does not move, and the cartilages holding the vocal cords transmit only a minimum of vibration to the body. This construction is like that described earlier for the ship's signaling system, in which two sound generators were combined in such a way that their diaphragms moved in opposite phase.

With an air stream passing through the vocal cords vertical to the direction of vibration of the vocal cords, it is not possible to eliminate all vibration in the direction of the air stream. Because of the elasticity of the vocal cords, there remains some vibration of the supporting cartilage in the direction of the air stream. High-speed motion pictures of the vocal cords show clearly that the greater part of the vocal cords vibrates horizontally, but that the edges vibrate vertically. Since this latter movement is not a symmetrical one, it will transmit a movement to the head with its maximum amplitude in this same direction, that is, in the direction of the air flow.

Previous investigations have demonstrated that, for bone-conducted sounds at frequencies below 1500 cps (see pages 130 and 167), the skull vibrates like a rigid body. Therefore it is possible to measure the amplitudes of vibration in the different directions simply by placing a vibration pickup on the head, normal to the surface. In Fig. 6-59 the vibrations of the head are shown during phonation of the vowel $\bar{o}$ ($p\bar{o}l$). The upper curve *a* shows practically no vibration of the forehead, and the lower curve *c* shows practically no vibration of the temporal bones. The vibration pickup used was the type whose output is proportional to acceleration, and it registers only vibrations normal to the bone surface.* The large vertical component of the vibrations of the skull is caused not only by the vertical vibrations of the edges of the vocal cords, but also by the sound pressure in the mouth. This sound pressure does not produce a lateral vibration of the skull, because of the lateral symmetry of the head, but it does produce vertical vibrations of both the lower jaw and the skull.

It is possible that, besides the translational movements of the skull, there can be a rotation of the skull as a whole. To investigate this possibility, measurements were made of the rotation of the skull produced by a bone-conduction receiver. If the axis of vibration of a bone-conduction receiver does not go through the center of gravity of the head, a rotation of the head must appear in addition to the parallel movement, because the forces acting on the head then have a tangential component.

To make a comparison between the two types of vibration, a bone-conduction receiver with a cube-shaped vibrating body and a surface area of 1 sq cm was used to drive the skull first in a normal direction and then in a tangential direction, as shown in Fig. 6-60. The size of the surface in contact with the skin and the steady pressure against the head were the same in both cases. An auxiliary pressure in the normal direction was used when the movement was tangential. The difference in the threshold of hearing in the two cases was measured. Table 6-4 shows that, for a tone of 100 cps, the vibration transmitted is about 35 db greater in the direction normal to the head than in the tangential direction. For the higher frequencies this difference is reduced to 15 db.

In making the measurements it is necessary that the stiffness of the bone-conduction receiver be so great that in the normal and tangential positions the amplitudes of the vibrations are the same. This may be

* Type 761A vibration meter, made by the General Radio Company.

accomplished by adding a mass to the bone-conduction receiver or by making the spring in the receiver so stiff that the resonance frequency of the vibrating system is outside the frequency range of the measurements.

In these measurements the bone-conduction receiver was applied in such a way as to produce rotations of the head about its vertical axis, but there was little change in the values when the receiver was applied in

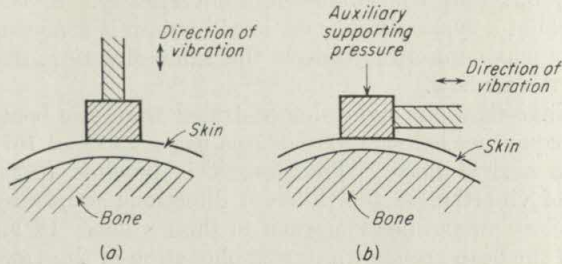


FIG. 6-60. Position of the vibrator (a) for producing vibrations normal to the surface and (b) for producing rotation of the skull.

a way that produced rotations about the horizontal axis. These measurements showed that the rotation of the head could be ignored whenever the direction of vibration of the bone-conduction receiver passed nearly through the middle of the head.

To investigate the rotation of the head during vocalization, two vibration pickups were placed on the temporal bone as in Fig. 6-61, and each pickup was connected to a pair of plates of a cathode-ray oscillograph.

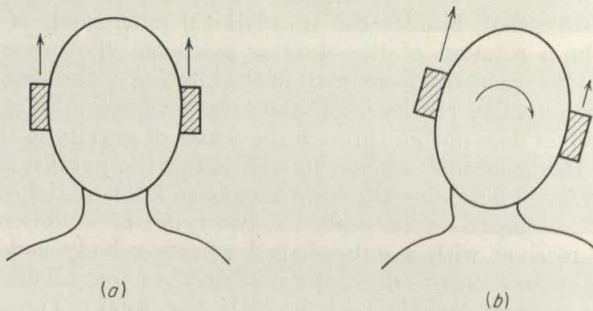


FIG. 6-61. Technique for measuring the rotation of the skull with two vibration pickups.

The direction of maximum sensitivity of the vibration pickups was parallel to the surface of the head. It was found that when the position of the head was symmetrical to the body, the phonation of z produced the same amplitude in the pickups on the two sides. The tilting of the head to one side reduced the vibratory amplitude on the side to which the head was tilted and increased it on the opposite side. The difference between the two sides was only about 10 to 20 per cent of the total vertical movement of the head. When the head was inclined about the axis going through the two ears, there was practically the same amount of

difference between the two sides. Because every vibration pickup is to some degree sensitive to air-borne sounds, the vibration pickups on the head were surrounded with a thick layer of cotton during the measurements.

TABLE 6-4

Frequency, cps	Threshold difference, db
100	35
200	32
400	20
800	17
1500	15
2000	15

For maximally useful hearing it is important to reduce not only the sounds of vocalization but also noises produced by chewing, swallowing, and the like. Even walking produces vibrations of the body that can be

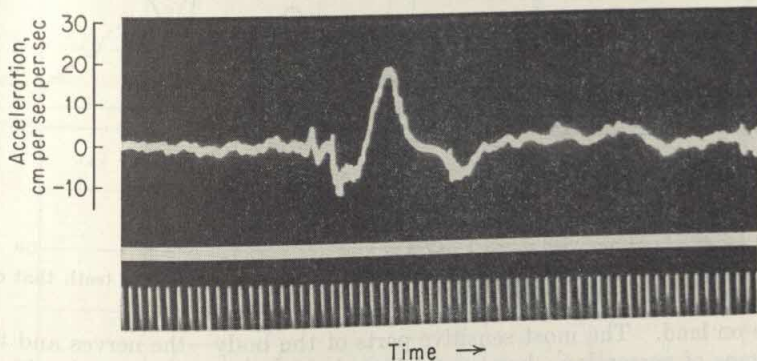


FIG. 6-62. Acceleration amplitudes of the head in the vertical direction during normal walking. The time marks represent thousandths of a second.

heard if the auditory meatus is closed, though the elasticity of the cervical vertebrae reduces these vibrations to some degree.* In Fig. 6-62 the acceleration amplitudes of the head in the vertical direction are shown for normal walking in a leather shoe.

Smallest Energy of Impact Audible by Bone Conduction. It is interesting to determine for every sense organ the smallest perceptible energy. For hearing by bone conduction the smooth surface of the tooth seems especially convenient for measuring this minimum mechanical energy. For this purpose a small pendulum was allowed to fall from a known height and to strike the surface of the teeth. This setup is shown in Fig. 6-63. With the mouth half open, the frame that holds the pendulum was brought within about 5 mm of the teeth. On the metal frame was a cross made from two wires having a thickness of 0.2 mm. The cross

* See the Author's Bibliography, Art. 33.

was held in a horizontal position by a forceps, and it tapped the teeth when the forceps was opened. From the weight G of the wire lying vertical to the axis of rotation and the displacement h of the center of gravity, the energy Gh can be calculated. In one case a wire with a weight of 1 mg was used to strike the upper teeth, and it was necessary for the center of gravity to fall 2.5 mm to produce a sensation of hearing. The measurements were made in an anechoic room and were repeatable. For the upper teeth the threshold energy was 0.2 to 0.5 erg for four subjects with normal hearing. In most cases the threshold for the lower teeth was the same. In one case it was 4.8 ergs.

The mass of the head, moved by this kinetic energy of 0.2 erg, is about 3.5 kg.

Role of the Eardrum in Sound Transmission. In the process of evolution it appears that mammals resulted from the adaptation of fish to a

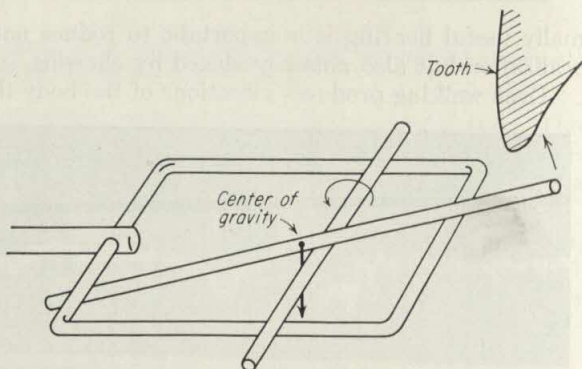


FIG. 6-63. Method of measuring the smallest energy of impact on the teeth that can be heard.

life on land. The most sensitive parts of the body—the nerves and the organs of perception—have not followed this adaptation completely, so that even in modern mammals these organs are embedded in a fluid of approximately the same composition that sea water had in earlier times. It is believed that the cochlea was developed from the lateral lines of the fish, and nowadays the cochlea still contains a liquid like sea water. This adaption to life on land created the problem in the ear of transmitting air vibrations to the fluid of the cochlea. From the purely physical point of view, a stretched membrane with a piston fixed in the middle of the membrane would seem to be the best solution.

Frank and later Esser made extensive calculations of the properties of the eardrum that give the best sensitivity and the widest band of transmitted frequencies. These calculations show that a light rod embedded in the membrane improves the coupling between the membrane and the piston without adding too much to the mass of the system.

The eardrums of various mammals are very different. Some eardrums resemble a stretched membrane, and others behave like stiffened pistons. Because these differences in structure are large it seems that the precise

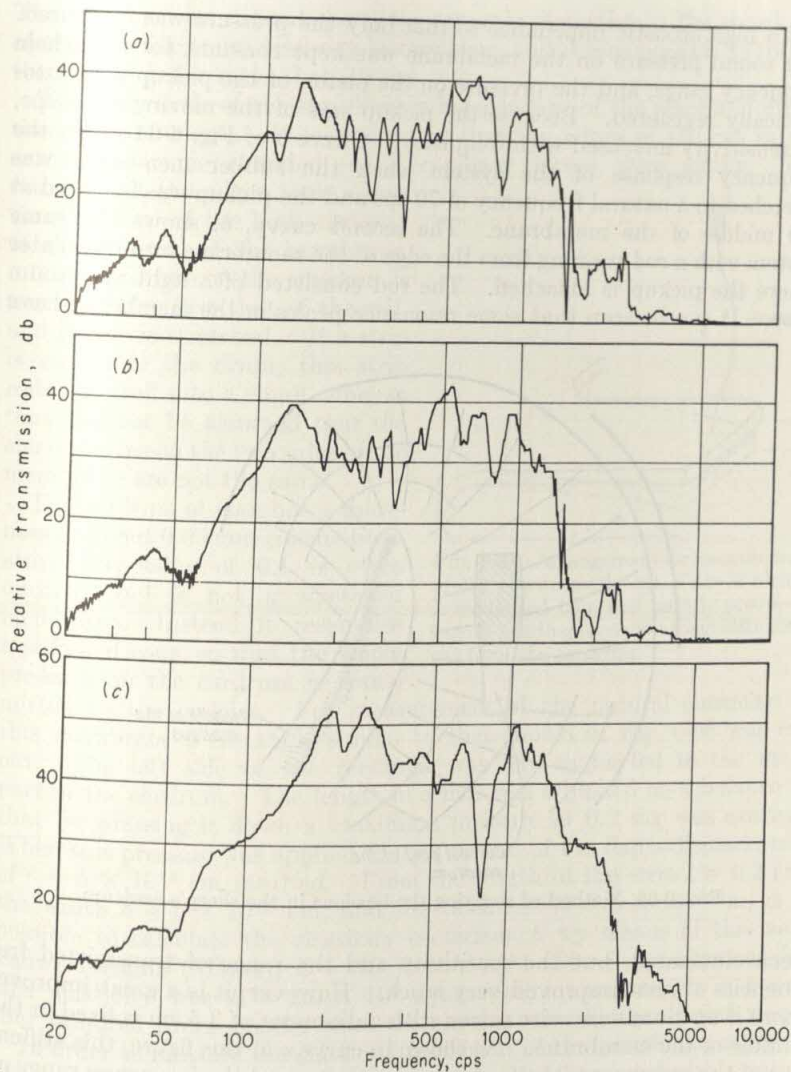


FIG. 6-64. Pressure transmission from an aerial sound to a piston fixed in the middle of a rubber membrane (a) without any stiffening of the membrane, (b) with an aluminum tube lying radially in the membrane, and (c) with a plate in the middle of the membrane.

arrangement of the eardrum is not critically important in the transmission of sound waves. Otherwise, similar structures would have been evolved.

To measure the degree of improvement effected by various changes in the eardrum, an artificial eardrum was constructed. It consisted of a rubber membrane 5 cm in diameter and fixed in the middle of a large metal sheet. The middle of the membrane was attached to a pickup that

had a high acoustic impedance so that only the pressure was measured. The sound pressure on the membrane was kept constant for the whole frequency range, and the pressure on the piston of the pickup was automatically registered. Because the pickup was of the moving-coil type, its sensitivity increased with frequency. Curve *a* of Fig. 6-64 shows the frequency response of the system when the rubber membrane was stretched to a natural frequency of 70 cps and the pickup was fastened at the middle of the membrane. The second curve, *b*, shows the same system with a rod running from the edge of the membrane into the center where the pickup is attached. The rod consisted of a light aluminum tube. It can be seen that some resonance peaks in the membrane have

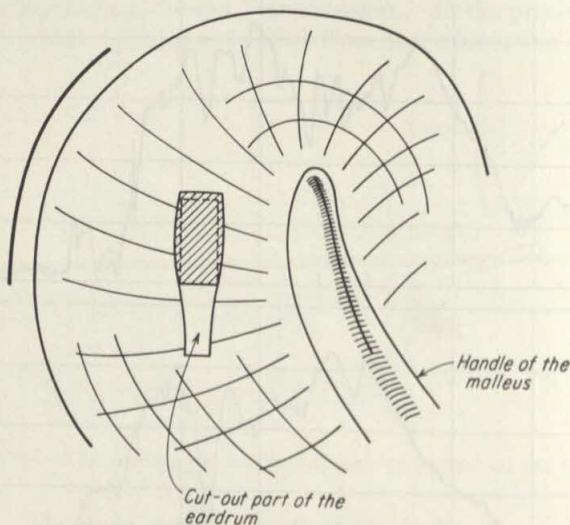


Fig. 6-65. Method of studying the tensions in the sheep's eardrum.

been eliminated, but the sensitivity and the range of transmitted frequencies are not improved very much. However, it is a great improvement if an aluminum wire screen with a diameter of 3.5 cm is fixed in the middle of the membrane. As shown in curve *c* of this figure, this stiffening of the membrane improves the sensitivity and the frequency range as well.

The eardrums of the calf and sheep are stretched membranes. The membrane of the calf, which is about 0.1 mm thick, consists of a kind of gelatinous film with a very great viscosity. This viscosity gives to the membrane a certain stiffness for rapid vibrations.

To estimate the tension in the eardrum, a U-shaped cut (similar to that shown in Fig. 6-65) was made in it with a special kind of scissors. The rectangle that was cut out was laid back and spread flat on the surface of the eardrum. From the barrel-shaped enlargement of the opening (as seen in the figure) it is possible to estimate the tension in the eardrum.

The flap that was cut out shows the converse distortion. The shrinkage of the flap due to its viscosity is very slow, and it was possible to follow the shrinkage for more than 10 sec.

The magnitude of the shrinkage is independent of the place and direction of the incision. It is interesting that the edges of the cut in the eardrum became rounded, as if capillary forces were acting. The rounding of the edges took a long time because of the high viscosity of the material of the membrane.

The eardrum of the chicken is much smaller than that of the calf, and it also is stretched. If a strip is cut from the drum, this strip rolls by itself into a small tube, so that it must be assumed that the elastic forces on the two sides of the membrane are not the same.

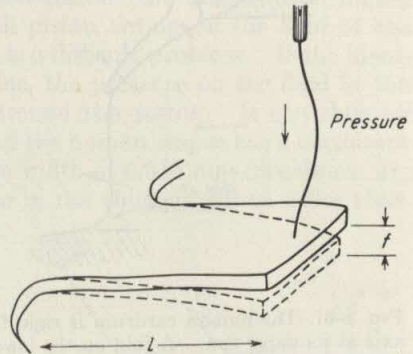


FIG. 6-66. Arrangement for measurement of the elastic coefficient of the eardrum. A calibrated hair was used to produce a known bending force on a tongue-like piece cut from the eardrum.

The eardrum of man has a thickness of about 0.05 mm (in the literature the value of 0.1 is often quoted) and is not a stretched membrane. Instead it resembles a stiffened cone, so that the whole pressure on the eardrum is transmitted to the ossicles. For measurement of the natural elasticity of this membrane a rectangle similar to that shown in Fig. 6-66 was cut out. The left side of the rectangle was left connected to the main part of the eardrum. The length of a hair was adjusted on a balance so that by pressing it down a maximum pressure of 0.2 mg was exerted. When this pressure was applied to the free end of the flap a displacement of $f = 5 \times 10^{-3}$ cm resulted. From the length of the strip $l = 0.2$ cm, the width $b = 5 \times 10^{-2}$ cm, and the thickness $h = 5 \times 10^{-3}$ cm, it is possible to calculate the elasticity coefficient E by means of the well-known formula (Marks), $E = 4P/fb \times (l/h)^3$. The value obtained for this elasticity was $E = 2.0 \times 10^8$ dynes per sq cm, which is about four hundred times smaller than the elasticity coefficient of pine wood.

In order to measure the elasticity coefficient of the gelatinlike eardrum of the calf a part of the eardrum was cut and rolled into a rod with a radius r . By having one end of this rod attached to the bony rim of the eardrum, it was possible to measure the bending of this rod for a known force applied to the free end. The elasticity coefficient can be calculated from the formula $E = 4P/3\pi r f \times (l/r)^3$, and the value obtained was 2×10^4 dynes per sq cm.

If the blood supply to the eardrum is stopped, the eardrum dries quickly because of its thinness. This can easily be shown by the change in the elasticity coefficient. Therefore it is important in its study to remove the middle ear as quickly as possible and to keep it in a chamber with controlled humidity until all measurements are completed.

The human eardrum consists of three layers, and the elasticity shows no changes with direction. The eardrum of a guinea pig is easily split in a radial direction, but its elasticity coefficient is about the same as in

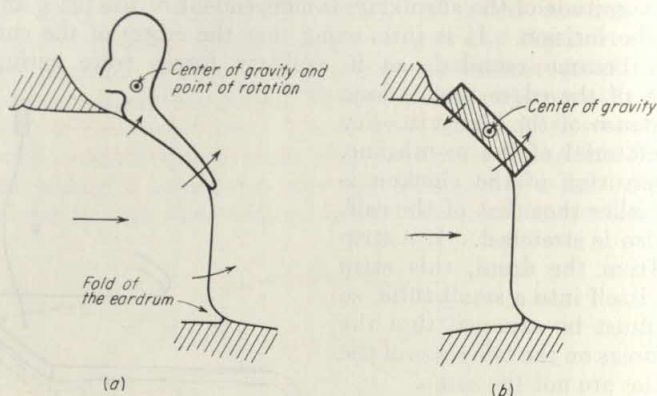


FIG. 6-67. The human eardrum is rigid for the lower frequencies and rotates on an axis at its upper rim. A fold on the lower rim permits movement of the rigid cone. In (a) the normal condition is shown, with the center of gravity and point of rotation the same; then no bending force acts to deform the conical shape of the eardrum. In (b) the head of the malleus is missing, and the center of gravity is below the point of rotation; then the conical shape of the membrane is deformed.

man and also shows no change with direction. The thickness of the eardrum of the guinea pig is 0.01 mm.

Because the human eardrum is stiffened so that it is like a piston, the question arises how the mobility of the eardrum at the rim is provided.

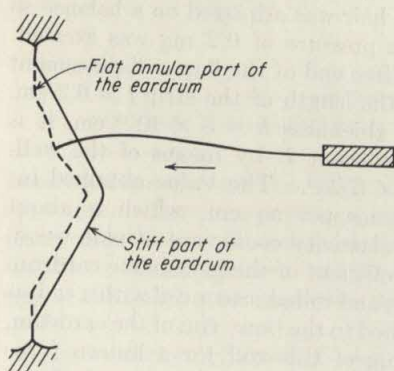


FIG. 6-68. The eardrum of the chicken is conical and rigid in the center. When it moves, its rim spreads out in a flat ring.

It was shown in earlier investigations (see page 101 and Fig. 6-67a) that in man the whole eardrum rotates about an axis above and tangent to its upper rim. Near the axis the movements are small and do not require a special elastic structure. On the edge of the drum opposite to the axis, in most specimens, a pronounced fold can be found that permits free movement of the cone.

A similar fold was not found in the guinea pig or the chicken, but if, as is shown in Fig. 6-68, the stiffened conical part of the eardrum is pressed toward the base of the cone, the edge of the drum forms a flat ring. The diameter of the cone is reduced at the same time. This special kind of elastic deformation of a stiffened cone can be reproduced on a cone made from a rubber sheet. From this description,

together with the measurements on the artificial eardrum, it appears that the shape of the eardrum in mammals is nearly optimal for the transmission of sound pressure to a system of high impedance.

Role of the Ossicles in Aerial Transmission. As the fluid in the cochlea is much denser than air, it is necessary to have a middle-ear mechanism that transforms the movement of a piston with a large surface area (the eardrum) to the movement of a small piston (the stapes) with higher pressure. Figure 6-69 shows a small piston acting on the fluid of the inner ear. The sealing of the piston is a difficult problem. If the membrane around the piston is too flexible, the pressure on the fluid in the cochlea will cause it to flow back around the piston. It can thus be understood why the membrane around the human stapes has a maximum width of only 0.1 mm and a minimum width of 0.015 mm (Stuhlman, 2). It is also obvious why the membrane in the chicken can be wider than

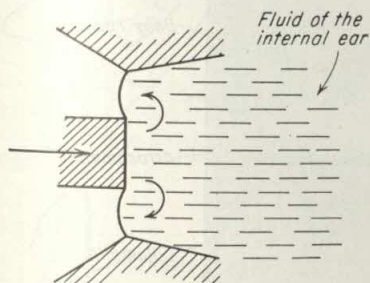


FIG. 6-69. The stapes must be surrounded by a very narrow membrane so that when the stapes moves inward the fluid does not flow in the direction of the arrows.

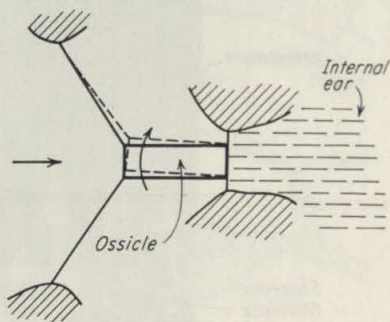


FIG. 6-70. In this simple form of middle ear, subharmonics (undertones) would be produced by rotational vibrations of the ossicle around its footplate.

that of man: the chicken has a cochlea with a length of only 5 mm, whereas man has one of 35 mm, and hence the forces due to inertia are much smaller in the chicken than in man. Since it is necessary to have a rigid piston to act on the fluid in the cochlea, and since it was found that for the eardrum a conical membrane gives a maximum sensitivity, a simple physical construction of the middle ear would be a system such as that shown in Fig. 6-70. The bony part around the internal ear must have a reasonable thickness to protect the inner ear. This gives the ossicle a minimum length. The length of the ossicle is greater than the width of the surface transmitting the pressure.

This system is not optimal for the transmission of air-borne sounds. If the eardrum is under negative pressure, so that the eardrum and ossicles are pulled outward, the system has only one degree of freedom. For a positive pressure, however, the ossicle is in unstable equilibrium and can tilt in various directions so that it has three degrees of freedom. This causes undertones (page 477). The eardrum moving in from left to right tilts the ossicle upward from the middle position (as shown in Fig. 6-70). When the movement of the eardrum is outward (to the left), the ossicle

comes back to the middle line. The next inward movement of the eardrum causes the ossicle to move downward because its kinetic energy carries it through the middle position. Therefore it is evident that during a full period of movement of the eardrum the ossicle makes an excursion to one side only. It moves with half the frequency of the eardrum.

To suppress these lateral movements of the ossicle, it is necessary to have an attachment to the bony wall as near as possible to the free end of the ossicle. This attachment ensures the movement of the ossicle in a single path. The ear of the chicken is constructed on this principle

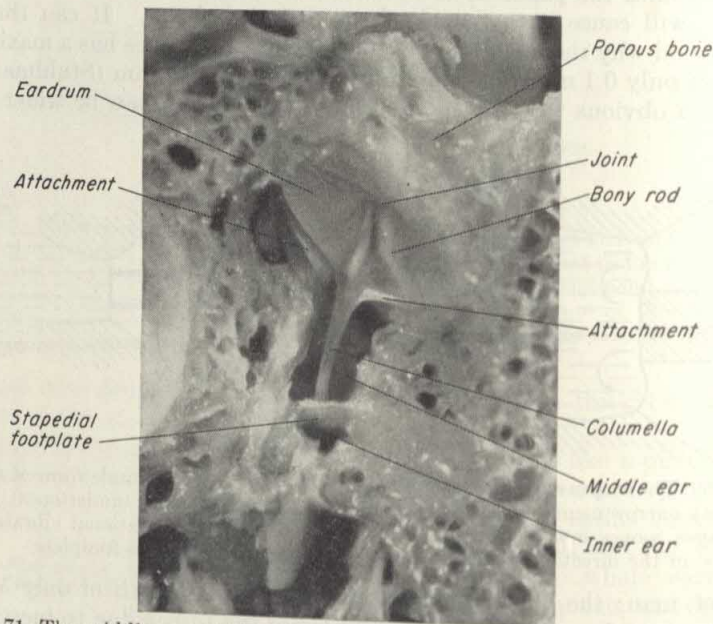


FIG. 6-71. The middle ear of the chicken. The cone of the eardrum is pointed outward, not toward the inner ear as in most mammals. The long ossicle (columella) is attached to the sides of the cavity. The bony rod lying on the eardrum corresponds to the handle of the malleus in mammals.

(see Fig. 6-71). To suppress the lateral movement it is advantageous to have a long ossicle. The best type of attachment would be by means of rigid rods lying in the eardrum at right angles to each other. This is precisely the construction that we find in the ear of the chicken.

Suppression of the lateral movements is necessary because the rigid rods have a low natural frequency, and, in general, there is slight damping. Every transient therefore would produce a dull thump. From the physical point of view it would be a better solution not to attach the ossicles in the middle of the eardrum but to suppress the lateral movements by having a small rod lying radially in the eardrum and then to attach the piston to this rod. This type of middle ear with two bones (the stapes and incus appear, in this case, to move as one bone) can be

found in the frog (*Rana pipiens*), as shown in Fig. 6-72. If we grasp with forceps one of the bones in the middle ear of the frog we can easily feel that there is only one degree of freedom in its movements.

Position of the Ear in the Bones of the Skull. In accordance with the principle that bone conduction should be minimal, the following paragraphs will describe the properties of the middle ear that bear upon this requirement. In looking for the best position for the middle ear in the skull we suppose that it would be best to have it as deep in the skull as possible to give it maximum protection.

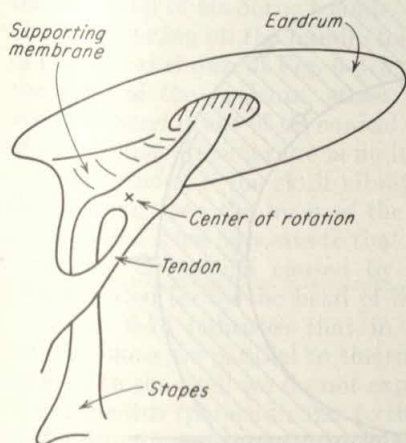


FIG. 6-72. The middle ear of the frog (*Rana pipiens*) has a piston fixed near the rim of the eardrum.

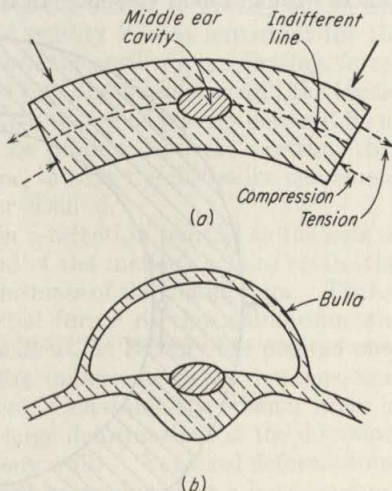


FIG. 6-73. Methods of minimizing bone conduction by locating the middle ear near a stressless zone of the skull wall. In (a) the location is in the indifferent zone of a thick wall. In (b), where the wall is thin, the stress is minimized by means of a bulla.

It is well known that hearing by bone conduction can originate in the middle ear in two different ways: (1) when the head is moved the inertia of the ossicles produces a movement of the ossicles relative to the cochlea, and (2) a motion, transmitted to the skull, deforms it in such a way that a relative movement is produced between the ossicles and the cochlea.

If we bend a rod in the manner shown in Fig. 6-73a, the lower half of the rod is compressed and the upper half is extended. In the middle of the rod is a line which is neither extended nor compressed; its length does not change during the deformation, and only shear stresses are set up. This situation is characteristic not only of rods but of other shapes as well. In Fig. 6-74 is represented a ring under pressure from the two opposite sides. The resulting tensions and compressions at different points on the ring are represented by the size of the arrows. Near the middle of the ring there are no tensions (Frocht).

In order to minimize hearing by bone conduction it would seem reasonable to decrease the magnitude of the deformation by placing the middle ear in a zone not subject to tension, as indicated by the cross-hatched area in Fig. 6-73a.

In animals whose skulls have thick bony walls, such as the ox or man, we find this type of placement of the middle ear. When, on the other hand, the size of the middle ear is greater than the thickness of the bony wall of the skull, this placement is no longer possible. The thickness of the bony wall of a full-grown cat, for example, is about 0.5 mm in the places without blood vessels. In this case tensions on the middle ear can

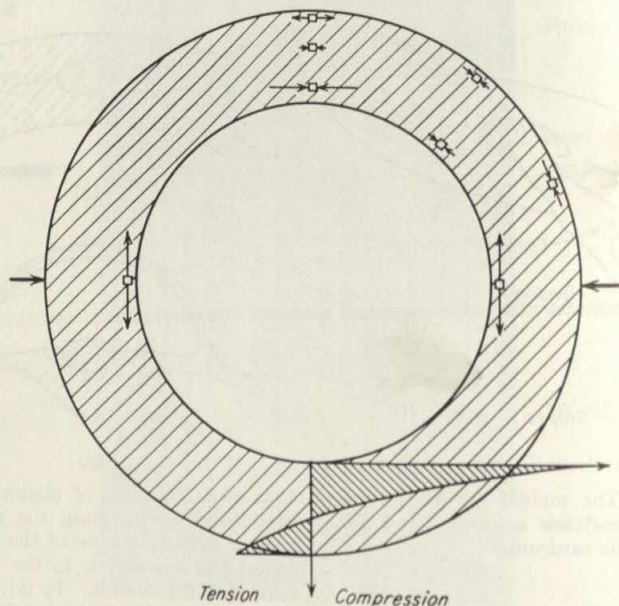


FIG. 6-74. Forces of tension and compression in a ring squeezed from opposite sides (large arrows). The small arrows show the direction and magnitudes of the internal stresses.

be minimized by surrounding it with a capsule. This capsule, which is called a bulla, is shown in Fig. 6-73b and is found in most small mammals such as dogs, cats, mice, etc. At the same time the bulla serves as an air space behind the eardrum and guarantees the mobility of the eardrum. In an arrangement of the type shown in Fig. 6-73a the necessary air volume behind the eardrum is maintained by the porousness of the bony wall surrounding the middle ear. The cochlea itself is protected against deformation by being coiled into a spiral. In mammals having a thick skull wall the cochlea is embedded in petrous bone. In mammals with a thin bony wall, the cochlea projects into the free air space of the bulla so that no deformations are caused by stresses in the bony part.

Does the Construction of the Ossicles Minimize Hearing by Bone Conduction? The foregoing discussions have shown that a rod in the

eardrum with the point of rotation on the rim of the eardrum helps to suppress undertones. As the ear should presumably be sensitive to a wide range of frequencies, we expect the mass of this rod to be as small as possible. But in Fig. 6-67*a* we can see that in the human ear the rod lying in the eardrum is loaded on one end with a large mass, called the head of the malleus. At first glance this mass seems to be superfluous. Bárány has pointed out, however, that the malleus and incus are constructed in such a way that the center of gravity and the point of rotation are the same. With the center of rotation near the edge of the eardrum, a head on the malleus is required to bring the center of gravity out to this point. This position of the center of gravity is also important for the transmission of air-borne sounds. When the eardrum is vibrating, forces of inertia acting on the handle tend to turn the handle around the center of gravity as shown in Fig. 6-67*b*. If the center of gravity does not lie at the edge of the eardrum, stress will be produced on the eardrum that tends to bend it out of its conical shape, so that the pistonlike movement of the stiffened membrane is no longer ensured.

Furthermore, if the skull vibrates in a direction parallel to the axis of the meatus, then the mass of the head of the malleus acts to rotate the malleus in a sense opposite to that of the mass of the manubrium. Therefore, the movements caused by inertial forces of the manubrium are compensated for by the head of the malleus, as Bárány has pointed out.

Figure 6-74 indicates that in a ring under stress the tensions and compressions are parallel to the surface. Consequently, when a stress is applied to the skull we do not expect large deformations in the direction of the meatus (perpendicular to the bony wall). Yet local deformations in the direction of the meatus might well be produced by a bone-conduction receiver placed near the meatal opening. During phonation the middle ear seems to be well protected against vibration and deformation in a direction parallel to the axis of the meatus.

Further consideration, however, indicates that this type of protection is hardly necessary. As Fig. 6-59*c* shows, during phonation the vibration of the skull is minimal in the direction parallel to the axis of the meatus and maximal in the vertical direction. Therefore the middle ear must be constructed in such a way that hearing by bone conduction caused by the vertical vibration is also minimized in an even more effective way. To prove this a small rod was attached parallel to the axis of the manubrium of the malleus of a fresh human specimen. An attempt to move the malleus in the three rectangular directions of a coordinate system showed that a displacement of the manubrium of the malleus in the direction of its long axis does not cause a displacement of the fluid in the cochlea. Furthermore, as Fig. 6-75*b* shows, a vertical displacement of the joint between the incus and stapes does not displace the fluid in the cochlea, because the footplate of the stapes merely rotates around its long axis and the movement of the fluid consists only of a displacement from the upper to the lower edge of the stapedial footplate. The normal movement of the stapes for air-borne sounds is shown in *a* of this figure. In order to minimize the displacement of the fluid during the start of

rotation of the stapes shown in *b* it seems important to have the footplate of the stapes as narrow as possible.

Because the large amplitude of vibration of the head during phonation is in the vertical direction, we should expect that the long axis of the footplate of the stapes would be at right angles to the vertical axis of the neck. This is the position we actually find in man and in the other mammals

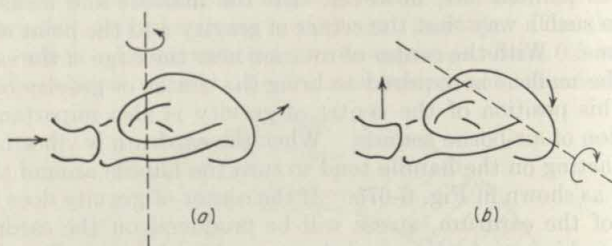


FIG. 6-75. The movements of the stapes. In (*a*) is shown the normal motion of the stapes to air-borne sound. When, as in (*b*), the movement communicated by the incus is vertical, the stapes rotates about its long axis and does not produce a displacement of fluid in the cochlea.

observed. On the other hand, it was found that in the frog and in the chicken the ossicles are not balanced and the malleus does not have a compensating head: the footplate is round and not elliptical.

If the ossicles of the human ear are moved in a horizontal plane at right angles to the axis of the ear canal, it can be seen that this movement also does not produce a displacement of the fluid in the cochlea, because

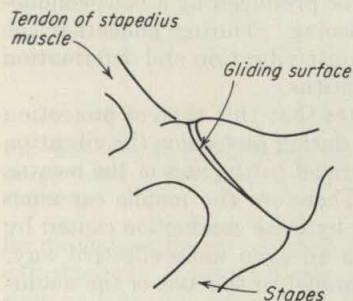


FIG. 6-76. The flat sliding surface of the joint between incus and stapes in the ear of the calf.

the joint between the stapes and incus is extremely flexible. Figure 6-76 shows that this joint in the calf is essentially flat. This can be seen especially well when the ossicles are dried so that the membranes have shrunk. The joint is definitely easier to slide in the direction of the axis of the footplate of the stapes than in the other directions.

By compression of the middle ear the ossicles are displaced relative to the wall. To minimize, in this case, the displacement of the fluid in the cochlea, it is important that the stiffness of the membrane around the footplate of the

stapes be greater than that of any of the other elastic parts of the middle ear. Thus the displacement of the ossicles occurs before the vibrations reach the cochlea.

From the discussions of these two principles, namely, that the transmission of air-borne sound should be optimal and that at the same time hearing by bone conduction should be minimal, it has been possible to outline many physical conditions that have to be fulfilled in the middle

ears of the most highly developed mammals. The agreement between these requirements and the actual construction of the middle ear gives us greater understanding of the peculiar structures of the middle ear. Still many questions remain unanswered: specifically the necessity for the middle-ear muscles other than as a protection against intense sounds. In man if we put a loud high-frequency tone in one ear, the muscles in both ears contract. Except for a small change in the impedance of the eardrum (see page 72) the writer has not been able to find a physiologically important change in the other ear. Voluntary contraction of the tensor-tympani muscle has about the same effect (Geffcken).

In spite of these unanswered questions, it is clear that in evolving the ear nature has utilized sound physical principles. In terms of these principles it is possible to account for many peculiarities in the structure and arrangement of the parts of the middle ear.

PART 3

THE PSYCHOLOGY OF HEARING

CHAPTER 7

AUDITORY THRESHOLDS

JUST-NOTICEABLE DIFFERENCES OF AMPLITUDE AND FREQUENCY*

Nearly all of the ear's characteristics, such as the threshold of sensitivity and the threshold of feeling, exhibit extraordinary variations as a function of frequency, often varying more than a hundred or a thousand times. For the development of auditory theory it is important to know whether this frequency relation depends upon different attributes of the nerve fibers supplying the various regions of the basilar membrane. If it is the physical characteristics that are important and we can consider the nerve fibers along the basilar membrane as behaving in a completely uniform manner in response to the stimulating pressures, then we can entertain the hope that an exact understanding of the physical process of sound transmission in the ear will lead to a solution of this problem of frequency relations, just as has been true in communications engineering.

There is nothing in the evidence from anatomy to contradict the assumption that the nerve endings along the basilar membrane are all alike. A microscopic study of these nerve endings, as well as of the brain cells, reveals no structural differences. There cannot be many chemical differences either, for no variations have been found in the staining qualities of the endings in the different regions of the membrane.

The determination of just-noticeable differences of amplitude, or the difference limen, appears to be a particularly suitable way of obtaining quantitative information on the nature of nerve excitation. The relative difference limen, which is the relation between the just-noticeable change of amplitude ΔJ and the amplitude level J , or $\Delta J/J$, is entirely independent of the quality of the ear's transmission system and hence is purely a neural characteristic. This is obvious because both tones that are being compared, with the amplitudes of J and $J + \Delta J$, have the same transmission factor which cancels out in the quotient. For ordinary loudnesses a change of amplitude of 10 per cent is perceptible, and so the two tones to be compared are but slightly different in intensity. Therefore, even in a nonlinear system such as that of the ear, the transmission factor is altered to such a slight extent as not to play any role. Preliminary tests showed that the changes of the threshold caused by the consumption of alcohol, the injection of cocaine, and fatiguing with intense sounds were always accompanied by changes in the difference limen. Thus we can expect that when the difference limen is invariable with

* Article 4 as listed in the Author's Bibliography. Published in 1929.

frequency the other characteristics of nerve excitation will be independent of frequency also.

It is important to establish, however, that these observations only indicate whether the nerve fibers behave in a uniform way, and they do not show whether there are interactions among the various groups of fibers, such as a contrast effect, which might be different for every frequency (see below, page 417). This might be so because the extent and form of the region of stimulation on the basilar membrane may vary for every frequency, and these observations do not take such a variation into account. The difference limen may prove to be independent of frequency, and yet for the various frequencies there may be differences in

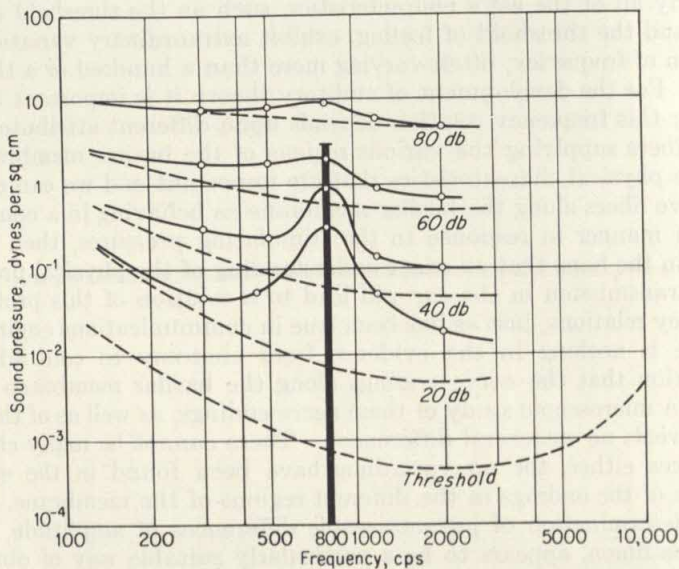


FIG. 7-1. Equal-loudness curves under normal conditions (broken lines) and after fatiguing the ear with a tone of 800 cps at 3 dynes per sq cm for 2 min (solid lines).

nerve excitation that are to be ascribed to contrast effects. Here would come into play all the influences that alter the form of distribution of stimulation along the basilar membrane, such as beats or the simultaneous action of a number of tones.

The two most recent measurements of difference limens, carried out by Knudsen (1) and Riesz (1) with modern technical facilities, have given directly contrary results on the frequency relations. Therefore the various physiological disturbances need to be taken into account at the outset.

Method of Determining the Difference Limen. Among these disturbing effects an important role is taken by aural fatigue. As indicated elsewhere (page 357), the loudness of a constantly presented tone can be greatly altered by fatigue. As an indication of the degree to which the frequency relations may be influenced, the equal-loudness curves were

considered. A tone of 800 cps was presented to one ear at a given number of decibels above threshold, and another tone of different frequency was presented to the other ear and adjusted in intensity until it seemed of the same loudness as the 800-cps comparison tone. The broken curves of Fig. 7-1 show the sound pressure in dynes per square centimeter that various tones must have in order to appear equal in loudness to the comparison tone, when this tone is presented at 20, 40, 60, and 80 db above threshold. Such curves have already been presented by Kingsbury.

One ear was then fatigued for 2 min with a tone of 800 cps at an intensity of 3 dynes per sq cm, and for the various tones the levels were found that seemed equal in loudness to the comparison tone. These results are represented in the solid curves of the figure.

The circuit used for carrying out these measurements is shown in Fig. 7-2. There were two oscillators G_1 and G_2 and three attenuators b_1 , b_2 ,

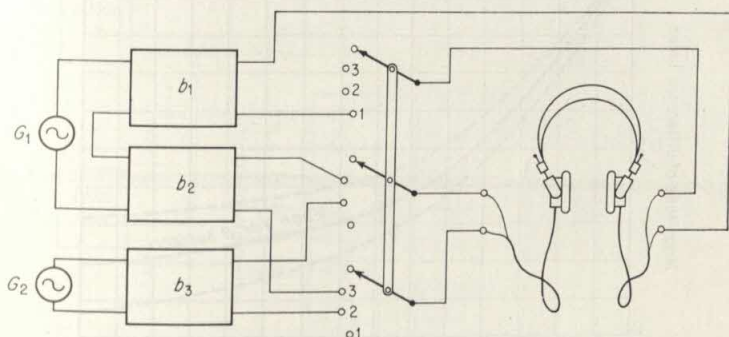


FIG. 7-2. Circuit used for determining equal-loudness relations after fatigue.

and b_3 , connected as shown. The switch was first thrown to its lowermost position, and a comparison tone of 800 cps was delivered to the phone on the right ear. Attenuator b_1 was adjusted to obtain the threshold. Then by appropriate settings of b_1 the comparison tone could be given amplitudes of 20, 40, or more db above threshold. Attenuator b_2 was used in the second procedure to deliver this same tone to the left ear as a fatiguing tone. In this procedure the switch was thrown to the third position for 2 min; then without any pause it was thrown to the second position to deliver the variable tone to the left ear. This tone was compared with the 800-cps tone in the right ear. By switching back and forth and adjusting attenuator b_1 , equal loudness was obtained, usually after four to six trials.

The displacements of the curves due to this amount of fatigue disappeared in 10 to 15 min, and the values returned to the ones shown by the broken lines. However, after measurements that continued for a month or more, mostly with the same comparison tone of 800 cps, there developed a clear and lasting disturbance, especially for faint tones. The disturbance was such that a change in intensity after the ear was fatigued produced a greater loudness change than was formerly the case.

Thus the difference limen was made smaller. [This effect may be regarded as an artificial recruitment.]

The temporal course of the difference limen following fatigue is shown in Fig. 7-3 for a tone of 800 cps and an intensity of 10 dynes per sq cm. Here the solid line shows mean values and the broken lines the extremes for eight subjects. These measurements were carried out with a rotary potentiometer giving sinusoidal changes of intensity at a rate of four per second. This rate was such that the intensity variations were not noticeable at the moment that the tone was switched on, and yet the duration was sufficient for them to be heard. Because the measurements were relative, it was satisfactory to take as a criterion for the audibility of the variations not the value at which they were just noticeable, because

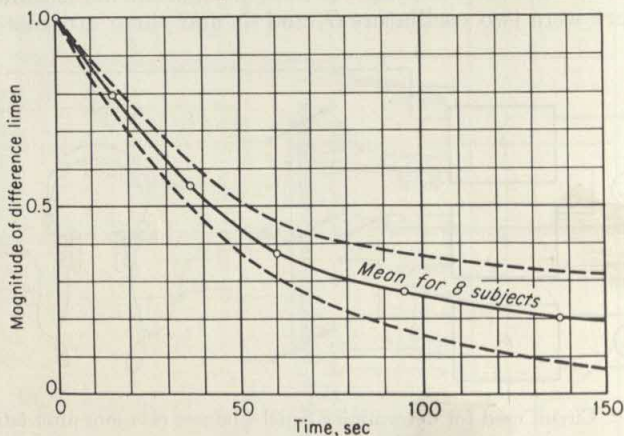


FIG. 7-3. Temporal course of the difference limen after fatigue. The solid line represents the mean of eight subjects and the broken lines the extreme values.

this value was greatly altered by wanderings of attention, but a certain larger value that could easily be held in mind during a series of measurements. Such a procedure can always be adopted for relative measurements, and it gives only a moderate dispersion of the data. It might be supposed that a fatiguing of the nerves would at the same time produce a change in the attentional conditions and hence an alteration of the difference limen, but this did not happen. The amplitude of the variations was such as to make them audible after about 2 min. The subject was not informed of the purpose of the experiment and was instructed to concentrate strongly every second on whether the variations were audible. The moment at which the variations became noticeable was exactly the same as if he had waited for 1.5 min after the tones were turned on and then had attended to the variations.

It was established further that the amount of the fatigue in the frequency region from 400 to 2000 cps was not significantly different, though of course it decreased as the sound intensity was reduced. It was the same regardless of whether the varying tone was listened to with one ear

or with both ears. If one ear was fatigued with a given tone, there was no effect upon the difference limen of the other ear.

The great effect of fatigue shown here makes it clear that it is better to measure the difference limen for loudness by presenting two brief tones in immediate succession, as just described, than to use the procedure employed by Knudsen and Reisz, who gradually increased the variations of a continuous tone until they became noticeable.

The difference limen was obtained by the following procedure as used by psychologists, and is known as the method of constant stimuli (see Pauli, 1). One of the tone pulses was kept constant, and the other pulse was given one of a series of different intensities. This series had its mid-point equal to the constant stimulus, and extended by uniform steps above and below it until the largest and smallest values were clearly

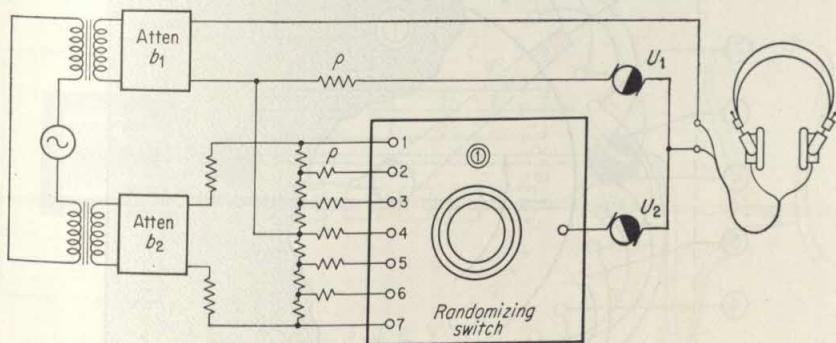


FIG. 7-4. Circuit used for measurements of the difference limen.

distinguishable from the constant stimulus. When comparisons are made for the whole series of stimuli, the middle values give judgments of equality and the end values give differences of greater and less. When the difference limen increases, there will be an increase in the number of intensity steps that give judgments of equality, and when the limen decreases, this number is decreased. Thus the difference limen is proportional to the number of equal judgments Σe and depends also, of course, on the steps ΔS between successive stimuli. If every stimulus in the series is presented n times, a just-noticeable change of amplitude $\Delta J = \Sigma e \Delta S / 2n$.

It is desirable to choose ΔS so that the number of equal judgments remains as nearly uniform as possible for all subjects and conditions, for then the errors arising from wanderings of the attention will remain the same for all the measurements. Otherwise it would be necessary to take account of the dispersion of the equal judgments and its effect upon the limen.

The circuit used for these measurements is shown in Fig. 7-4. The oscillator worked through two transformers into two attenuators, one, b_1 , to determine the intensity of the constant tone, and the other, b_2 , for the series of comparison tones. Attenuator b_2 worked into a matched

resistance whose middle portion was separated into six equal steps. Depending on the step to which the phone was connected, a voltage was added to or subtracted from the base voltage of attenuator b_1 , thereby determining the intensity of the comparison stimulus. The rotating switches U_1 and U_2 were used to alternate the two stimuli.

The size of the steps in the stimulus series was governed by attenuator b_2 . By changing both attenuators the same amount, the intensity level was changed without changing the relative size of the steps. As the attenuators changed the intensity in logarithmic fashion, they could cover the whole loudness range. Resistor ρ was a correction value, so chosen

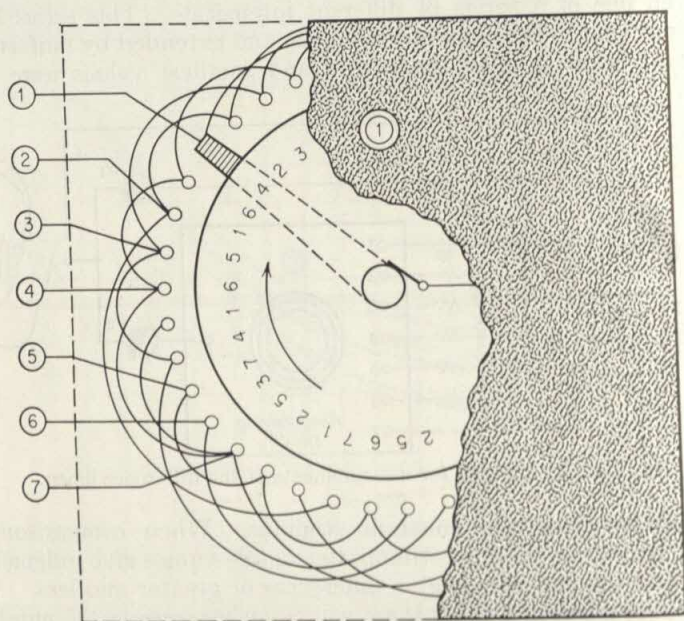


FIG. 7-5. Randomizing switch.

that the resistance as seen from the phone was the same for all settings of the step switch.

It was important that the subject remain without knowledge of his results, and in order that he might operate the apparatus himself a randomizing switch was provided as shown in detail in Fig. 7-5. As the knob was turned, the seven steps appeared in an irregular order.

The measurements were carried out in the following manner. A button was pressed that set into operation switches U_1 and U_2 (which were in another room). After the loudness judgment was made, the randomizing switch was advanced to the next position, whereupon a number appeared representing the stimulus pair that had just been given. A record was then made for every stimulus as to whether it was judged louder, equal, or weaker relative to the standard. For the final measurements, however, the numbers were covered so that the subject was entirely ignorant of

them. After every comparison a button was pressed that operated one of seven counters that recorded the number of equal judgments for this stimulus. Another counter recorded the number of presentations, and indicated when this number reached 70 for each stimulus. Then the number of equal judgments was read off and entered into the above formula. In this arrangement it was only necessary to be sure that the stimulus steps were sufficiently large that the two end stimuli were always judged correctly, for otherwise the formula does not hold. This simplification of the procedure made it possible to obtain more than 50,000 judgments for each subject.

For the final measurements the phones were replaced by the apparatus shown in Fig. 7-6, because the low tones in particular were rich in overtones at the larger amplitudes. This apparatus consisted of an electrodynamic loudspeaker with an acoustic filter in front of it, from which the

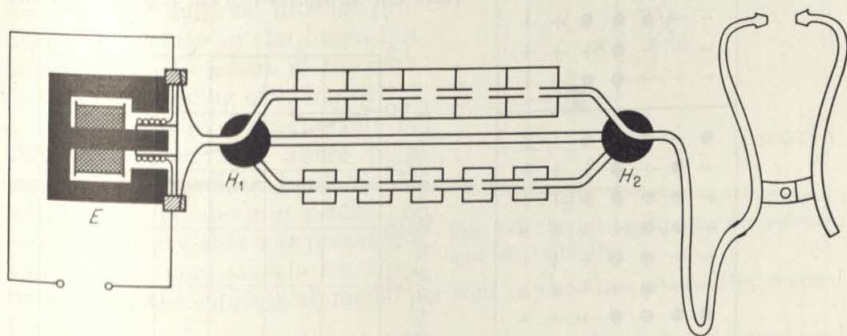


FIG. 7-6. Loudspeaker with an acoustic filter.

tone was conducted to the ear through a hard-rubber tube. This filter could be switched out by means of stopcocks.

The difference limen did not depend upon the duration of the individual tone pulse. As was shown earlier, even weak tones attain their maximum loudness within 0.3 sec after they are switched on. Hence a duration of 0.5 sec was chosen for the tone pulses.

The interval between the members of a comparison pair has only a limited effect also. According to Köhler's theory of successive comparison, the making of a comparative judgment consists merely in the appearance in consciousness of an impression of a rise or fall of intensity (Köhler, 2). Hence a judgment of intensity difference can be made without any consideration of the tonal character or the absolute intensity. This impression of rise or fall depends on the degree of agreement between the neural effect persisting from the first pulse and the effect arising from the second one. Inasmuch as this process remains the same, the difference limen is the same also. If the interval between the two pulses is made long, there will appear a gradual deterioration of the first neural effect, and then the second pulse that is physically equal will be perceived as louder. Then, however, the physically weaker stimuli will be perceived

as equal in loudness, and the total number of equal judgments will remain the same. Also a long interval between pulses can produce various kinds of irregularities in the neural effect, and therefore a wide dispersion of the equal judgments. Even so, their number is unaffected. This stability of the judgments is indicated in Fig. 7-7, which represents

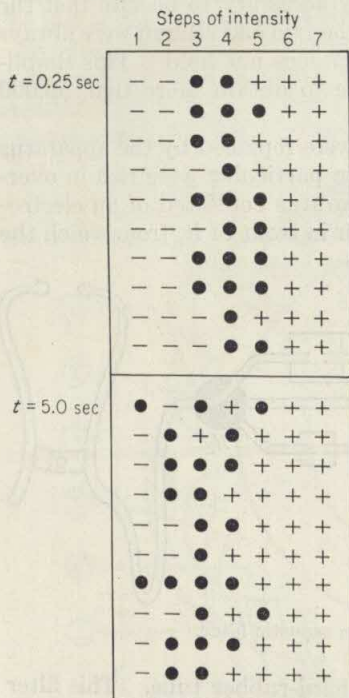


FIG. 7-7. Simple protocols for two time intervals between the pulses.

some of the protocols obtained. The dots represent equal judgments and the signs + and - represent judgments of the second pulse as respectively louder and weaker than the first. Here the first tone pulse was followed by a second one after 0.25 sec and a third after 5 sec, with the last two being compared with the first. It is clear that the longer interval has caused the

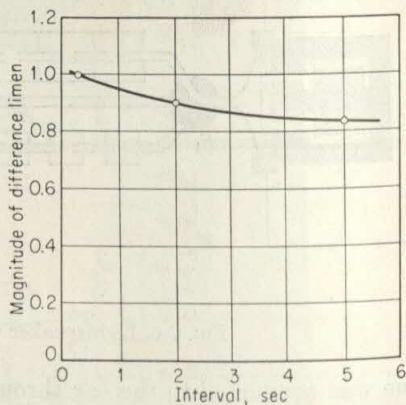


FIG. 7-8. Effect on the difference limen of varying the interval between pulses, in an unpracticed subject.

equal judgments to be shifted toward the smaller intensities of 1, 2, and 3. Also the dispersion is noticeably greater, for apparently the making of the first comparison has impaired the second. Even so, the number of equal judgments is unaltered.

This agreement with the theory holds only for practiced subjects, however. In general, persons who have not previously carried out this sort of observation will show a slight reduction of the limen as the interval is lengthened, as shown in Fig. 7-8. With practice this variation rapidly disappears. The reason is that an unpracticed subject requires a certain amount of time to separate out, among the many phenomena that a tone pulse presents, the particular ones pertinent to a loudness comparison. The correctness of this assumption can readily be established by adding some sort of disturbing effect to the tone pulse, as by loading the diaphragm of the loudspeaker with a small weight. Then at the beginning

and end of the pulse there is added a damped tone representing the natural frequency of the loaded diaphragm. If the interval between the two pulses is great, the damped wave train can readily be distinguished from the true pulse, and no change in the limen is observed when the disturbing sound is filtered out. But if the second pulse follows closely on the first, there is a marked reduction of the difference limen. This happens because the damped wave train has a different amplitude depending on the phase at which the varying current is switched on, and as a result the number of equal judgments is reduced. If the disturbing effect is removed by means of an acoustic filter, the difference limen becomes larger. Preliminary experiments showed that for all subjects an interval of 1 sec was sufficient, and a longer interval did not produce any change in the limen but gave greater dispersion of the data because of a fading of memory.

It was further brought out in this experiment that there is a capacity of absolute loudness as well as one of absolute pitch. A sound intensity that was presented two or three times could be matched by most of the subjects about 80 per cent of the time even after several hours.

To prove that a gradual onset and decay of a tone pulse, as produced by the acoustic filter, had no effect upon the results, the difference limen was determined by using both rectangular pulses and pulses with gradual onsets and decays. The circuit of Fig. 7-9 was used to deliver these pulses. Here the grid voltage of the final amplifier tube of the oscillator was maintained at a high negative value so that the voltage across the resistor ρ was not transmitted. But when switch U was opened for a moment the condenser C was gradually charged through resistor R , and the grid voltage was thereby diminished, permitting the tube to amplify in a normal manner until a closing of U again switched it off. By choice of the values of C and R the rate of the amplitude changes could be controlled within wide limits. If switch S was operated briefly, the condenser was momentarily charged and the tone pulse had an abrupt onset. Repeated measurements with various frequencies showed that switching S in and out did not alter the difference limen.

The difference limen remained the same if one tone pulse was delivered to one ear and the other to the opposite ear. In this dichotic presentation it was important to make sure that the interval between the pulses was as long as possible, so that the effects produced by the two pulses would be well separated. Then the pulse in the one ear was least affected by the foregoing action of the pulse in the other ear. If the interval was

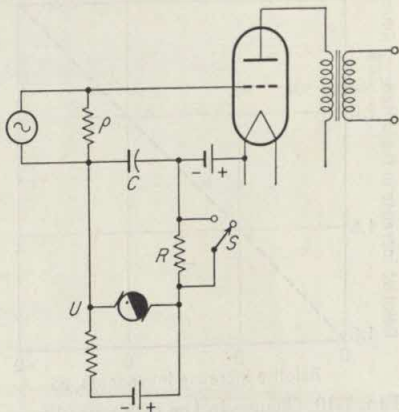


FIG. 7-9. Circuit for turning the pulse on and off gradually.

5 sec, then even in untrained subjects there was agreement of the results within 2 per cent, whereas an interval of 0.5 sec gave a threshold whose mean value was 17 per cent smaller for dichotic presentation.

The limen was determined also by presenting the two pulses to one ear and at the same time stimulating the other ear with two pulses of the same frequency and of equal intensity. This procedure gave larger limens because the loudness of the base was increased and then a greater loudness

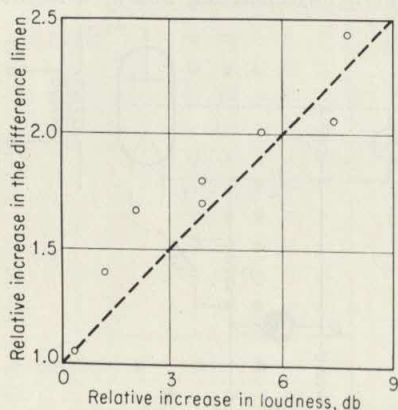


FIG. 7-10. Change in the difference limen caused by applying a tone of the same frequency to the other ear at various intensities so as to vary the total loudness.

change was required to be perceived as different. Some of these results are given in Fig. 7-10. The abscissa shows the apparent rise in loudness produced by stimulation of the other ear, and the ordinate shows the factor by which the limen was increased.

It is of interest to note in this connection that the change of loudness is always attributed to the ear in which the stimulation is the greater. This is true even if the stimulation in this ear is constant and it is varying in the other ear. If the intensity is the same in the two ears, the changes of loudness are always referred to the middle of the head. The difference in stimulation of the two ears had to

be at least double the normal value of the difference limen in order to give a certain localization to one side of the head or the other.

No effect on the difference limen was found on an alteration of the tension produced by the middle-ear muscles. It was established by Kato that contractions of these muscles are always bilateral. It was possible to deliver an intense high-frequency tone such as one of 5000 cps to one ear, thereby producing an active contraction, without causing any change in the difference limen measured in the other ear for a low tone such as 100 cps. This observation shows both that the limen is unaffected by the muscle contraction and that there is no effect of stimulation of the opposite ear by a tone well separated in frequency from the one being measured.

The Difference Limen for Amplitude and the Equal-loudness Curves. The final measurements of the difference limen were made at two levels, 20 and 40 db above the threshold of the 0.5-sec tone pulses. The median values of a large number of series obtained on several subjects are shown in Fig. 7-11. Here it is evident that the difference limen is independent of frequency over the entire range from 50 to 12,500 cps. The upper curve represents values obtained at a level of 20 db above threshold, and the lower curve those at 40 db above threshold.

That neural stimulation is of the same nature at all these frequencies is

further indicated by the fact that the difference limen has the same magnitude when measured for two successive tones of different frequency. It has already been shown by the equal-loudness curves in Fig. 7-1 that two tones of different frequency that are equally loud do not in general lie at the same level above their own thresholds. If they did, then the

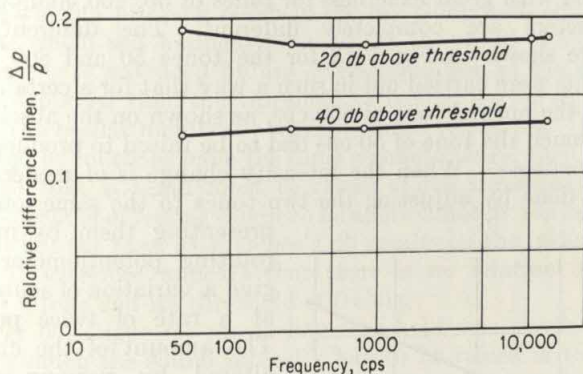


FIG. 7-11. The difference limen as a function of frequency, obtained at two loudness levels.

curves as plotted on a logarithmic scale would run parallel to one another. Hence the difference limens do not remain constant along the curves of equal loudness. In order to obtain difference limens of intensity for tones of different frequency, it was necessary first to equate the comparison tone in loudness to a reference tone. The reference used here was 800 cps. Then it was found what variation was necessary in the comparison tones in order to perceive them as different from the 800-cps tone. The relative values obtained by this procedure are shown in Fig. 7-12. It is evident that the difference limen is independent of the tones being compared.

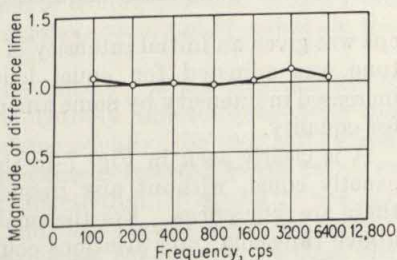


FIG. 7-12. Relative magnitudes of the difference limens obtained by comparing tones of different frequency.

Further evidence for the uniformity of neural stimulation comes from the fact that for all frequencies a raising of the sound intensity by a given number of decibels has the same effect upon the difference limen, as also may be seen in Fig. 7-11.

It is now clear that though moderate changes of intensity have the same effect upon the difference limen at all frequencies, this is no longer true when the changes of intensity are great. The equal-loudness curves plainly show that for the low tones a given decibel change produces a greater change in loudness than for the high tones. The curves of equal loudness are not produced merely by incidental physiological conditions.

Since the tones being compared are separated more and more in frequency, it might be assumed that the differences of character of the tones are responsible for this phenomenon, but this is not the case. The equality in loudness of two tones is a true equality, and two tones that are equal to a third tone are equal to one another. This fact may be demonstrated with great exactness for tones of 50, 400, and 5000 cps, as their characters are completely different. The different loudness increases are shown in Fig. 7-13 for the tones 50 and 800 cps. The measurements were carried out in such a way that for a certain intensity increase for the normal tone of 800 cps, as shown on the abscissa, it was found how much the tone of 50 cps had to be raised to produce the same change in loudness. When the intensity change is of moderate degree this can be done by adjusting the two tones to the same loudness and

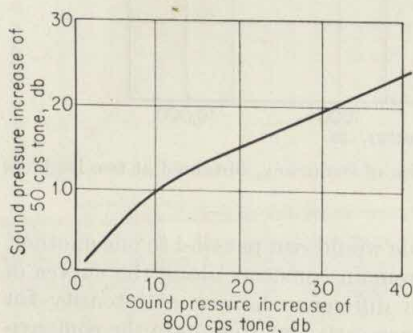


FIG. 7-13. Equal-loudness level increases for two tones differing widely in frequency.

presenting them by means of a rotating potentiometer so as to give a variation of sound pressure at a rate of twice per second. The amount of the change was altered by varying a parallel resistance. With most subjects this method becomes inexact when the sound intensity is raised to high levels. Therefore a direct comparison was made of the values of sound pressure increases producing equal-loudness changes for two successive tone pulses. For this purpose the tone of 800 cps was given an initial intensity of 40 db above threshold, and the 50-cps tone was adjusted for equal loudness. Then the 800-cps tone was increased in intensity by some amount and the 50-cps tone again adjusted for equality.

It is clearly seen in Fig. 7-13 that up to 6 db the two tones remain exactly equal, without any frequency effect. For still larger changes there are differences. For the smaller loudness levels, up to about 30 db above threshold, no variations could be found, and this fact is obvious from Fig. 7-1, where the lowermost curves run parallel to one another. Hence it is improbable that these variations arise from differences among the nerve fibers. It is more likely that new phenomena enter when the loudness is raised to higher levels.

It may be that interactions between nerve fibers arise for low tones at high levels as broad areas of the basilar membrane are stimulated. The effects may be similar to what happens in the eye on the presentation of two patches of light of equal intensity but different size; here the larger patch seems brighter than the smaller. All subjects report that when a tone of 50 cps is increased in intensity it changes its timbre, and this is true even when the tone is completely pure. Hence it is probable that the nonlinear characteristics of the ear play a part. Though for

high tones the vibratory amplitudes of the eardrum are small because of the large elastic forces acting upon it, the same pressure variations at low frequencies produce large displacements that bring in nonlinear actions to an important extent, and the transmission is no longer proportional to the applied sounds.

If the sound intensity of a tone is gradually increased, a level is finally reached at which a pricking is felt in the ear along with the tone. The intensity at which this happens is called the threshold of feeling. As a similar pricking is produced by any overstimulation of the nerve fibers, it may be supposed that the threshold of feeling serves to protect the endings of the basilar membrane against excessive sounds. If the nerve fibers excited by all tones have the same characteristics, then the amount (in decibels) that a sound must be raised above threshold in order to reach the threshold of feeling ought to be approximately the same. However, this is not the case, as Fletcher's (2) results on the feeling threshold indicate. It therefore appears that there is no relation between the loudness of a tone and its threshold of feeling.

The effect of fatigue on the feeling threshold was studied by determining how much the sound intensity had to be raised in the course of 1 min so that the pricking continued at a uniform level, and at the same time the falling off of loudness was observed. It was found that the loudness fell off much more than the threshold of feeling, which for most subjects was hardly affected. In one subject a curious effect was found in that the pricking periodically appeared and disappeared at the rate of about once per second. If the sound intensity was increased further, this phenomenon appeared throughout the whole frequency range, while the variations of the threshold of feeling became steadily greater. This phenomenon suggests that the threshold of feeling probably results from a stimulation of nerve endings in the middle ear and not of endings in the basilar membrane.

In support of this explanation is the fact that when only one ear is stimulated the buzzing is localized at an entirely different place from the tone. Also, when both ears are stimulated equally, the tone is localized in the middle of the head, while the pricking is referred to the two ears separately. In this connection it was found that, if a tone in one ear was raised to the threshold of feeling and then the other ear was stimulated with a strong tone of the same frequency, the over-all loudness was increased, whereas the pricking did not seem to be any greater. Moreover, the level of the threshold of feeling in one ear was not affected if the other ear was stimulated with a tone that was even above its own threshold of feeling.

These tests were carried out by means of the circuit shown in Fig. 7-14. To avoid the sensation of dizziness that appears when an intense tone is suddenly switched on, a resistance R was used to give a gradual increase in the voltage from the oscillator. Switch S was used to turn on the tone in one receiver or the other, or in both. Resistance ρ was used to adjust the intensity in one receiver so that the threshold of feeling was reached in both ears for the same current, which could be used as a measure of

any changes in this threshold. The most satisfactory frequency for these measurements was 200 cps, because for this tone the loudness at the threshold of feeling is reasonably small, as compared for example with that for 800 cps, for which it becomes unbearable. This fact itself shows that the feeling threshold does not correspond to a curve of equal loudness.

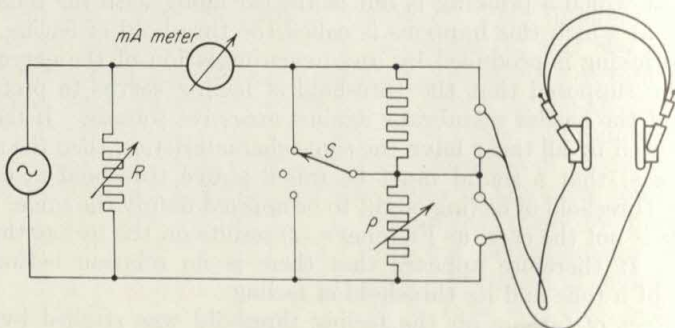


FIG. 7-14. Circuit for the study of phenomena at the threshold of feeling.

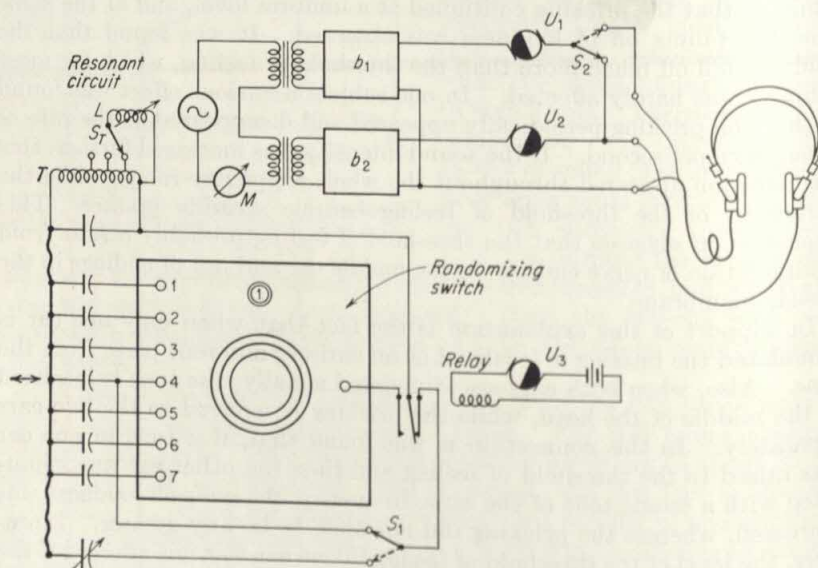


FIG. 7-15. Circuit for the measurement of frequency discrimination.

Relations between the Difference Limens for Amplitude and Frequency. Now that it seems likely that the nerve excitation at different regions of the basilar membrane is much the same, it is well to inquire into the frequency relations of the difference limen for frequency. The determination of this limen was made in much the same manner as just described, by comparing the frequency of two successive tone pulses. For this purpose the circuit of Fig. 7-15 was used. Stepwise changes of

frequency were produced by adding small condensers of appropriate values to the main condenser in the oscillator circuit. These condensers were made of old air condensers arranged with their plates on a common shaft, and the number of plates varied, one for the first step, two for the second, and so on. Thus the steps of frequency Δn were uniform for the whole series. So that this array of small condensers could be used even at the low frequencies, the capacitance of the oscillating circuit was stepped down by means of an autotransformer T . By this means the apparent impedance of the condensers was greatly reduced, with the same effect as if the capacitance had been correspondingly increased. The switch S_T was used to change the capacitance by large amounts and was adjusted so that the switching in of the small condensers always gave the same percentage change of frequency. This is a satisfactory condition for the measurements, because the difference limen $\Delta n/n$ varies only

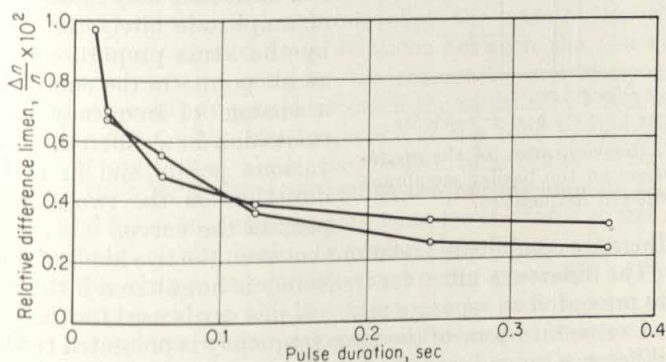


Fig. 7-16. Effects of the duration of the pulse upon pitch discrimination, for a tone of 800 cps at 40 db above threshold.

slightly with frequency. Minor adjustments could be made by rotating the common shaft of the condensers. A precise setting of the base frequency could be made by varying the inductance L of the oscillating circuit by shifting its iron core. An automatic relay was used to present the middle step as the first pulse and then some other step, chosen at random by a special switch, as the second pulse. The switching of the tones on and off was done by means of interrupters U_1 and U_2 . The ammeter M was used to check the current and make sure that it was not altered by the changes of frequency. When the thresholds were to be measured for both ears together, switch S_2 was placed in its upper position. It is possible for a given frequency to be heard as different in pitch in the two ears, and when this happened switch S_1 was used to change the frequency of the middle step so that the pitch appeared the same in the two ears.

A certain time is required for the perception of the pitch of a tone, and therefore preliminary tests were made to discover how the difference limen varied with the duration of the pulse for tones 40 db above threshold. These results are shown in Fig. 7-16 for two subjects and a tone of 800 cps.

For lower tones the curves continue to decline for even longer times, and therefore 1.0 sec was chosen for the pulse duration. Durations longer than this produce no changes in the difference limens. The same considerations as before governed the interval between pulses.

The fact, which Knudsen found, that small variations of frequency and

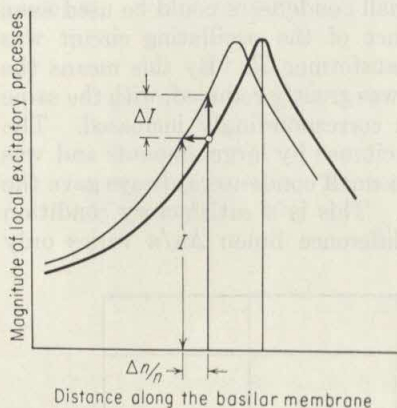


FIG. 7-17. Representation of the excitatory processes on the basilar membrane for two adjacent frequencies.

of amplitude can easily be confused may be understood by reference to Fig. 7-17. Here it is shown that a slight displacement of the curve of excitation such as may be produced by an alteration of frequency can only be perceived in terms of changes in the strength of excitation at the various points. There is a difference only in that a change of amplitude alters the excitation by the same proportional amount at all points in the curve, whereas a change of frequency alters the excitation in a different way at the various points and in a different direction on the two sides of the peak of the curve.

Thus there are complicated relations between the two kinds of difference limens. The difference limen for frequency is not altered if the two tone pulses are presented to separate ears. If one ear is used for the measurements and a constant tone of the same frequency is presented to the other ear, the difference limen for pitch changes in accordance with the apparent loudness of the tone in just the same way as shown in Fig. 7-10 for the difference limen for loudness. Moreover, the percentage change in both difference limens remains the same as the intensity level is raised above the threshold. Because the basilar membrane is strongly provided with transverse fibers, a deformation produced at one place does not spread out with the passage of time as is usually the case for other tissues. For example, a weight placed upon the skin produces a deformation that is still spreading even after 30 sec. The stimulation curve for the basilar membrane has the same form even for longer actions of a tone. Since both difference limens depend upon the perceptibility of changes in the distribution of stimulation, and there is no change in the stimulation with time, it follows that both difference limens are affected in the same way as a result of fatigue. To test this point, an intensity modulation was superimposed upon the tone, and the size of this variation was chosen so that at the instant the tone was switched on the modulation was barely noticeable. When the modulation was reduced by some amount it became audible only after a little time, as shown in Table 7-1 for a tone of 800 cps at a sound pressure of 10 dynes per sq cm. The same sort of measurements were made also with frequency modulations, by using a rotating condenser with a rate of rotation of four times per second. The

TABLE 7-1

Relative size of the difference limen	Time required for perception of amplitude variations, sec	Time required for perception of frequency variations, sec
1.00	0	0
0.74	22	19
0.55	37	40
0.37	61	66
0.30	140	150

capacitance was adjusted so that the frequency modulation was just perceptible at the onset of the tone, and then was decreased and the times measured until the modulation could be perceived. As the table shows, the two kinds of modulation sensations follow the same course with time.

In order to bring out additional relations between the two difference limens, it is necessary to consider the schematic excitation curves of Fig. 7-17 and especially to note how much the excitatory effect is altered at a particular point when the frequency of the tone is changed. The distribution of excitation along the basilar membrane is continually sharpened up through interaction among the nerve elements as a result of contrast, and hence it is necessary to consider the form of this curve in the higher centers of the brain, or preferably at that place where the magnitude of the change of excitation is directly presented to consciousness. To a certain extent this condition can be satisfied by observing the increase in loudness when a tone of one frequency is presented to one ear and an equally loud tone of another frequency is simultaneously presented to the other ear. Then the combining of the two neural effects must take place in a higher brain region. We can then assume, without too great error, that there is only a negligible contrast effect arising in the pathway from the first coming together of the two excitations up to the point where the loudness change appears in consciousness. Hence the excitations arising in the two ears may simply be added. When the tones in the two ears are of the same frequency and loudness there need not be any doubling of the loudness, because the magnitude of the excitation that passes from one ear into the neural pathways of the other cannot be as large as the excitation in the pathways of this other ear itself.

In Fig. 7-18 is shown the equipment used for measuring the loudness increase when a tone in one ear is added to the equally loud tone of the same frequency in the other ear. At first the switch S was opened, and the attenuator b_3 was adjusted for equality of tones in the two phones. Then attenuator b_2 was set to the value just found for b_3 and switch S was closed, so that both phones sounded simultaneously; and the tone pulse following this one was altered by means of b_2 so that the tone produced by both phones together seemed of the same loudness as if only one were switched on. When the attenuators were properly adjusted, the ammeter I showed that the oscillator current was not affected by closing the

switches U_1 , U_2 , and U_3 . Results obtained for a number of subjects, for tones throughout the auditory range at 40 db above threshold, are shown in Fig. 7-19. This figure shows how much the loudness was increased when two ears were used as compared with one. The mean value of 4.1 db is altogether independent of frequency, as expected.

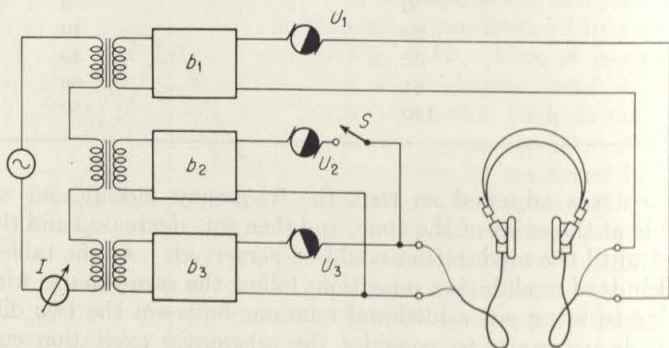


Fig. 7-18. Circuit for measuring the increase of loudness resulting from stimulating both ears with the same tone.

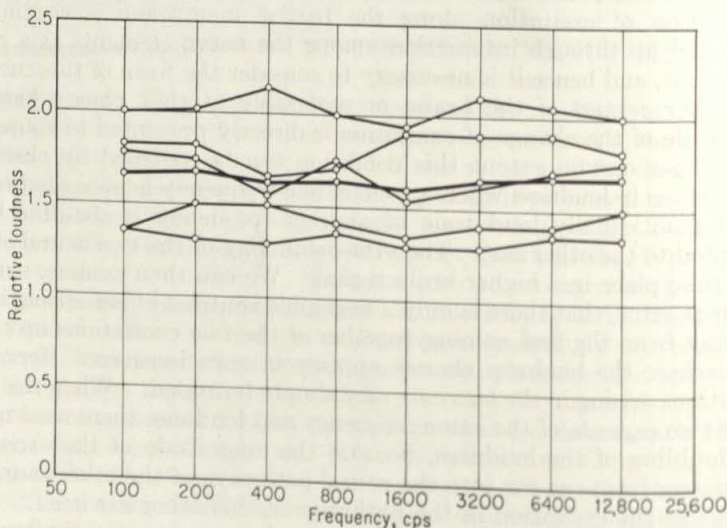


Fig. 7-19. The loudness increase produced by stimulating both ears with the same tone.

These measurements were carried out with phones covered with felt; so this increase in loudness cannot be an artifact caused by a conduction of the sound from one ear to the other. Furthermore, bone conduction was not involved, because the transmission of sound by bone is negligible relative to that by air. This is readily proved by use of the circuit of Fig. 7-18. The switch S was opened, and attenuator b_3 was set so that the loudness of the tone was equal in the two ears. If now the opening of the phone on the left was sealed over so that no sound could escape by

air conduction, it was found that the current into the phone had to be increased by means of attenuator b_3 by at least one thousand to ten thousand times in order to restore an equality of loudness in the two ears. The bone conduction produced by the vibration of the earphone case was smaller than the air conduction by this amount and hence was negligible. It is best to carry out these experiments initially with the smallest possible intensities, for otherwise the phone will be overloaded by the heavy current required after its opening is occluded. Then the contact of the diaphragm with the magnet will give erroneously low values. The results show that the relation between air and bone conduction is the same over the entire range of frequency and loudness. Also there are only slight differences among phones in this respect.

Stumpf (4) and Hornbostel (1) failed to find any loudness increase of this sort. Perhaps the reason was that they worked only with weak tones whose difference limens were so large that slight increases in loudness could not be appreciated with certainty. Certainly the results do not prove that the threshold is raised when both ears are used together. Indeed, at the threshold the difference limen is already so large that no effect is seen if there is a doubling of the loudness (a 6-db increase). This experiment is successful only if the subject works at the limit of his ability and a sufficient number of observations are made so that changes are revealed that are smaller than the difference limen. For this purpose the comparison tone in the one ear was changed by operating b_3 until it seemed barely louder, and then, beginning with larger values, until it seemed just softer, in order to arrive at a general indication of a middle value. These adjustments were concerned only with changes of loudness. The difference between increases of loudness and increases of tonal volume was clearly perceived at the moment that the tone was switched into the other ear. Therefore a confusion of these two attributes of the tone could hardly occur, especially as most of the subjects were accustomed to using various sorts of cues in their loudness comparisons, such as that of a click or a tone pulse.

It may be shown by means of the circuit of Fig. 7-20 that in fact the form of the excitation curve is unaltered by preliminary exposure to a continuous fatiguing tone. Measurements were made of the increase in loudness that results when an equally loud tone of a different frequency was presented to the other ear. This was done once without the preliminary fatiguing and then after the fatiguing. At first b_1 , which controlled the altered frequency from oscillator G_2 , was set so that the loudness was equal to that of the reference tone from G_1 . Then switch S was opened, and S_1 was set between the two middle positions. Now when S was briefly switched on, the two tones were sounded together by switching to the next-to-the-last position of S_1 . The loudness of these tones was compared with that of a tone obtained by switching to the last position of S_1 , and equality was arrived at by varying b_2 . From the settings of b_1 and b_2 the loudness increase was obtained. In order to find the loudness increase produced by preliminary fatiguing, the switch was turned to the second position for 2 min; then b_1 was adjusted with S open

so as to give equality of the tones in the two phones. Thereupon the fatiguing was repeated after a particular interval with S closed, and after 2 min a comparison was made of the loudness at positions 3 and 4 of the switch. The values obtained are shown in Fig. 7-21, where the open circles represent measurements made without fatigue and the filled

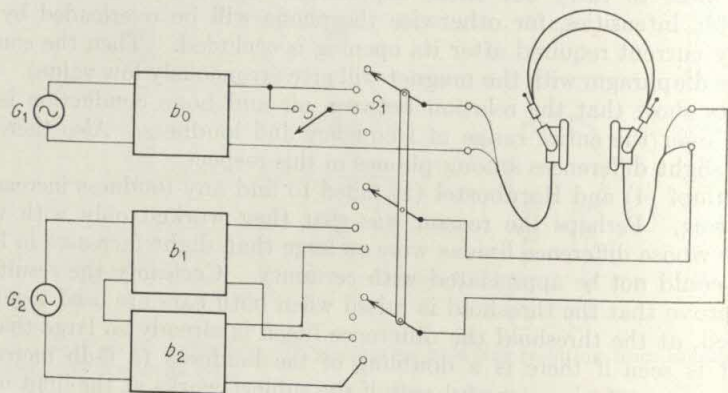


FIG. 7-20. Circuit used for adding a tone of a different frequency to the other ear.

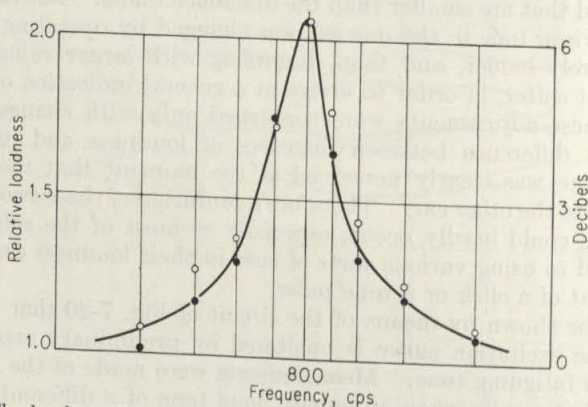


FIG. 7-21. The loudness increase produced by adding an equally loud tone of different frequency to the other ear, for normal conditions (open circles) and after fatigue (filled circles).

circles represent those made after fatigue. It is obvious that there is no effect of fatigue.

The increase in loudness that results when the other ear is stimulated with an equally loud tone of a different frequency was determined for various tones by using the circuit of Fig. 7-18 with a second oscillator operating into attenuator b_1 . This second oscillator delivered frequencies of $n + \Delta n$ when the one shown was delivering frequencies of n . In order to bring out most clearly the form of the increase in loudness as the frequency separation of the two tones was increased, subjects were used

that had already been found to experience the largest loudness increases when the tones in the opposite ear were equal. In these measurements it was found best to fix the attention of the subject in such a way that he regarded the variable frequency in the other ear as a disturbance that might alter the loudness of the base tone of constant frequency. The results, obtained with only a few subjects, are given in Fig. 7-22. All are for levels 40 db above threshold. The data obtained for 500 cps are in agreement with those already obtained by another method.

In considering the relation between the difference limen for amplitude variations and that for frequency variations, see Fig. 7-23 in which two

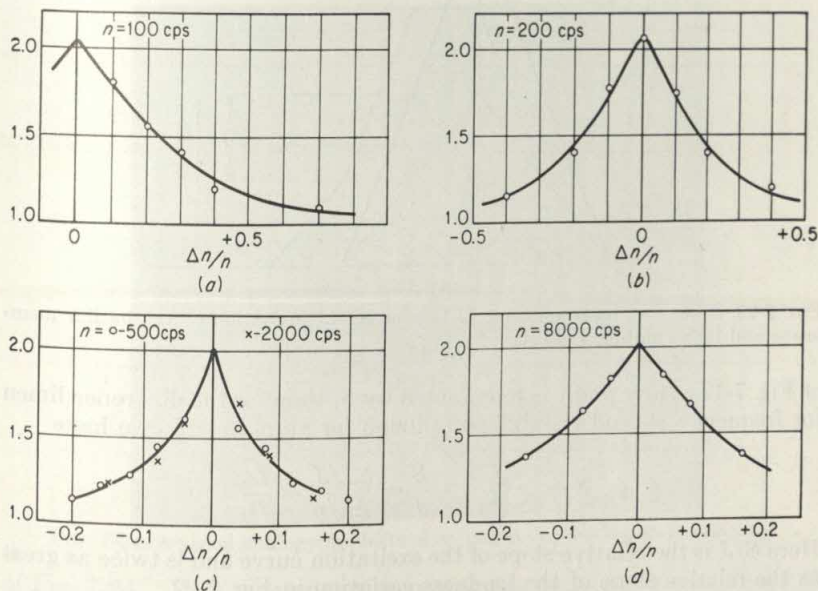


Fig. 7-22. Results as in the preceding figure, for additional frequencies. In graph *c*, the open circles represent 500 cps, and the crosses represent 2000 cps.

excitation curves for different frequencies are represented schematically as *a* and *a'*. Here it may be noted that under the conditions just stated, when the two tones are delivered to the opposite ears so as to give a doubling of the loudness, the relative decrease in the size of the excitation $\Delta J/J$ occurring at a place that is at a distance $\Delta n/n$ from the point of maximum excitation is twice as great as the relative decrease in loudness $\Delta L/L$. Hence the loudness is determined by the maximum of excitation. Because of the form of the curve, a shift along the frequency scale produces different amounts of change in excitation at every point. This fact is made clearer by a consideration of Fig. 7-17. The frequency shift of $\Delta n/n$ (that is, a change in frequency of $n \Delta n$) produces a certain change of excitation at the point indicated, but less at points to the left of this and more at points to the right, until the maximum of the first

curve is reached, and so on. This shifting of the curve of excitation becomes noticeable if at some place the relative change of excitation $\Delta J/J$ attains a value equal to the difference limen. The excitation curves show that the relative change $\Delta J/J$ produced by a slight shift in the upper part of the curve is nearly constant and represents a maximum, and therefore it is this upper part of the curve that is determinative of the perceptibility of a frequency change. If the slope of the excitation curve

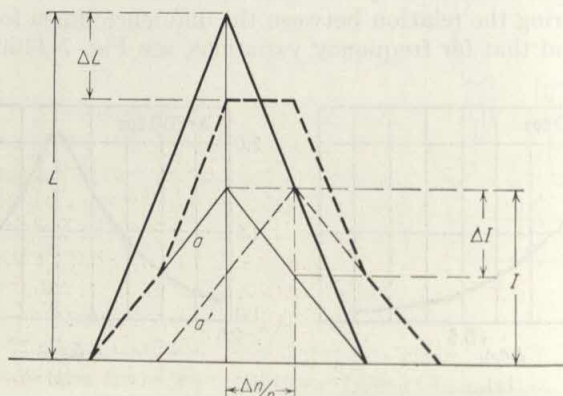


FIG. 7-23. Schematic representation of two curves of excitation on the basilar membrane and their combined effects.

of Fig. 7-17 at any point is represented by S , then for the difference limen for frequency D_f and the difference limen for amplitude D_a we have

$$S = \frac{\Delta J}{\Delta n/n} \quad \frac{S}{J} = \frac{\Delta J/J}{\Delta n/n} = \frac{D_a}{D_f}$$

Here S/J is the relative slope of the excitation curve and is twice as great as the relative slope of the loudness variation in Fig. 7-22.

If we use this equation for the measurements with 500 cps for example, we find that the relative loudness changes to $\Delta L/L = 0.5/2.0$ when the frequency is altered by $\Delta n/n = 0.043$. This relation can be obtained from the tangents of the curve on the upper left of Fig. 7-22. Therefore the relative slope of the loudness curve

$$\frac{\Delta L/L}{\Delta n/n} = \frac{0.5}{2 \times 0.043} = 5.8$$

and that of the excitation curve $S/J = 11.6$. We see here that the order of magnitude of one difference limen can be determined from the other.

From the frequency relations of the difference limen for frequency it can be determined, as Fig. 7-22 shows, that the slope of the excitation curve for a tone of 2000 cps is not significantly different from that of a tone of 500 cps, whereas the other frequencies show a smaller slope and

accordingly a larger value of the frequency difference limen, just as the measurements have shown. The fact that the difference limen that is derived from the steepness of the excitation curve is larger than that measured in terms of loudness increase signifies that from the place of crossing over of the auditory fibers to the locus in the brain where the loudness changes come to consciousness they must traverse a path in which a further sharpening up of the excitation curve is brought about through contrast.

That the ability to observe a shift in the excitation curve depends upon the amount of the decline in excitation is best shown in the visual analogy

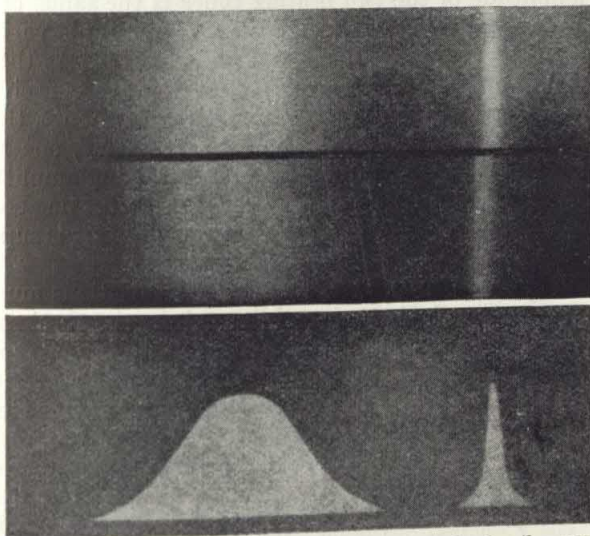


FIG. 7-24. A visual analogy of shifts of excitation on the basilar membrane.

of Fig. 7-24. Here the upper picture was obtained by rotating the lower one. A shifting of the upper picture is readily apparent at the right, where the thin line of light appears, and can hardly be seen on the left, where the lighted area is broad. Thus shifting of the region of stimulation is the more clearly seen the more rapidly the excitation falls off at the edges of the region. This relationship may seem obvious, yet it is necessary to emphasize it, for it is this just-perceptible spatial shifting of the curve of excitation on the basilar membrane that depends on the slope of the excitation curve and is different for every frequency.*

Theory of Beats. As a further application of the observation that the nerve endings along the basilar membrane are everywhere about the same, consideration will be given to the relations of beat phenomena to frequency. Because the movements of the basilar membrane are highly damped, the stimulation produced by a tone extends over a broad area.

* [Here two pages of the original paper have been omitted, in which speculations were made on the locus of maximal stimulation along the basilar membrane. The problem was later taken up experimentally (see Chaps. 11-13).]

It follows that two beating tones whose difference in frequency is small have regions of excitation that overlap to a large extent. If we represent the vibrations of two tones as having frequencies n_1 and n_2 and amplitudes A_1 and A_2 , then a simple calculation shows that we can regard the two beating tones as a single tone whose amplitude varies at a rate of $\gamma = n_1 - n_2$ but at the same time whose frequency at the moment of the beat varies back and forth about the value

$$\Delta n = \gamma \frac{2A_1A_2}{A_1^2 - A_2^2}$$

Now if the amplitude of the two beating tones is the same, or $A_1 = A_2$, there is no frequency variation along with the amplitude variation, and then the tone has a steady frequency of $(n_1 + n_2)/2$. As the idea of a tone of varying frequency is somewhat vague, we can conceive of beats between tones of unequal amplitudes ($A_1 > A_2$) as though the stronger tone A_1 consisted of two tones of the same frequency, one having the same amplitude as A_2 and another with the remaining amplitude. The first of these tones together with A_2 will then form a beating combination with the steady frequency $(n_1 + n_2)/2$, on whose beating is superimposed the second tone with the amplitude $A_1 - A_2$.

In order for the beats to be perceptible, the variations must attain a certain value. In Fig. 7-25 the dotted lines along the abscissa represent

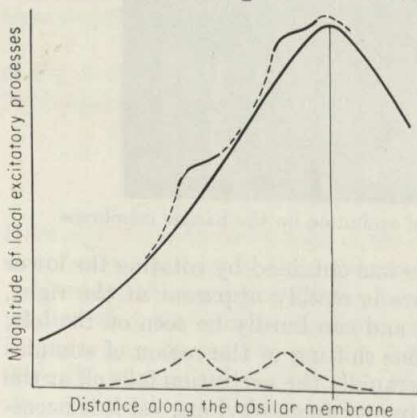


FIG. 7-25. Contrast effect in relation to beats.

the excitations corresponding to the two beating components for various beat frequencies, and the heavy curve represents the course of the excitation produced by the main tone with constant amplitude. If the deformations of the excitation curve produced by the superimposed varying effects are to be perceptible, it is not so much that these variations must attain a certain size relative to the size of the constant excitation but that by contrast the deformation must have a certain curvature, as indicated by the heavy-lined segments of the curves. Through

the contrast effect this curvature determines the sharpening up and accordingly the separability of the beatings from the continuing excitation. It is then clear that a limited deformation can give rise through contrast to a change of excitation that is larger than the excitation produced by the deformation itself.

Here it becomes apparent that there is a difference between the changes of amplitude that may be produced in a tone by back-and-forth movements of a potentiometer and those that arise when a second tone is made to beat with it. In the first situation the amplitude variations are

observable if they are as large as the difference limen, which has the same value for all frequencies. In the second situation, however, the relative magnitude of the superimposed tone that is necessary to give perceptible beats depends upon the relations of curvature of the excitation curve and therefore is different for every tone. The size of the curvature of the excitation curve depends upon its slope, which is inversely proportional to the difference limen for frequency, as already shown. Thus the relative magnitude of the second tone that is required to give perceptible beats must be greater the less the slope of the excitation curve or the greater the difference limen for frequency. Accordingly, it now is clear why

Riesz, who measured beat thresholds, obtained much larger amplitude changes for low tones than for high tones, when because of the constancy of the difference limen no differences with frequency were to be expected. It must not be forgotten that beats consist of frequency variations as well as amplitude variations, and both must be taken into account. To be sure, there is a proportional relationship between the just-perceptible amplitude variations in beats and the difference limen for frequency, as shown in Fig. 7-26.

Here Knudsen's measurements of the difference limen for frequency are represented along with Riesz's results on beats, both on a logarithmic scale. Therefore we can

suppose that in the determination of just-noticeable amplitude variations in beats it was the difference limen for frequency and not that for amplitude that was operative in producing the variations with frequency.

Moreover, the results of Riesz (1) plainly bear out the uniform nature of nerve excitation for all tones. If a logarithmic plot is made of the size of the relative difference limen for amplitude as a function of the sound intensity above threshold, as shown in Fig. 7-27, it becomes clear that the form of the curve is the same for all frequencies. Only 1000 cps shows a variation. However, because in the American telephone laboratories 1000 cps is used as a reference tone, just as 800 cps is used in Europe, it is probable that so many measurements have been made with it that a lasting fatigue has been produced leading to a hypersensitivity of the nerve endings, as may be seen in Figs. 7-1 and 7-3. At any rate, the same variation may be seen in the European measurements with 800 cps at low levels.

If the difference between the two tones is increased so that the beating rate rises, it is found that the size of the loudness variation decreases

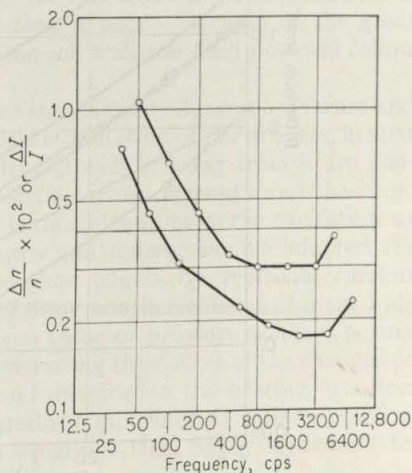


FIG. 7-26. Relation between the difference limen for frequency and just-noticeable changes of amplitude in beats.

greatly. This might be accounted for in part by the fact that the regions of stimulation are now more separated from one another, and the overlapping is less, whereupon the magnitude of the beating falls off.

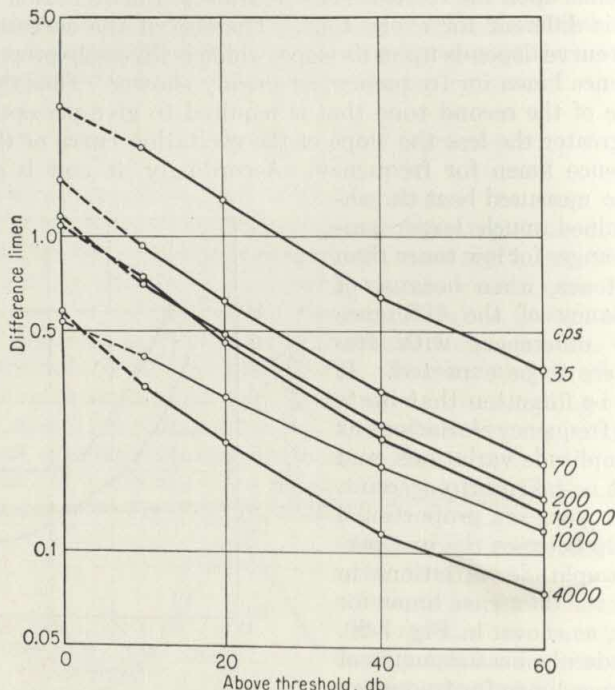


FIG. 7-27. Relative difference limens as a function of loudness level for a number of frequencies.

Yet the nearly aperiodic character of the basilar membrane motion makes this hardly possible. Moreover, Fig. 7-25 shows that a shifting of the excitation curves has little effect upon the relations of curvature, as the heavy-lined segments clearly indicate. Actually this decline in magnitude of the loudness variations with increased beating rate depends upon another phenomenon.

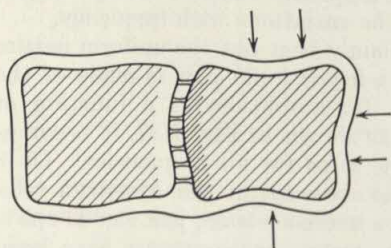


FIG. 7-28. Schematic representation of two adjacent nerve cells when exposed to a pressure gradient.

Let us consider, as shown in Fig. 7-28, two adjacent nerve cells in the basilar membrane that are exposed to a pressure gradient. In such a case the fluid of the cell exposed to the greater pressure will be pressed

through the cell walls into the other cell. Because the cell wall is semipermeable, substances dissolved in the cell fluid will not be able to pass through. Therefore there will be an increased concentration of the

substances in front of the wall, while on the other side of this wall there will be an accumulation of clear fluid. An increase of concentration in a cell produces an osmotic pressure, which with the elastic forces of the cell wall counterbalances the imposed pressure.

The difference in concentration on the two sides of the semipermeable wall must now be regarded as determining the magnitude of the excitation. In this regard it becomes obvious that only rapid pressure variations can produce a neural excitation, for then the concentration changes will not have time to be equalized through diffusion. If the pressure change lasts for only a brief time, we can probably assume that the quantity of fluid that passes through the cell wall will be proportional to the exerted pressure and the time that it acts. Because of the great frictional resistance of the pores of the cell wall the fluid flow will follow Poiseuille's law.

We come here to the same relations that Nernst (2; see also Nernst and Riesenfeld) postulated for the electrical stimulation of nerve fibers, in that the substances transported up to the cell wall or away from it are considered to be proportional to the electric current strength and the time. Nernst's formula, which indicates the magnitude of nerve excitation as the effect of various current strengths and pulses, can be adapted for present use as an expression of pressure effects by replacing current strength by pressure gradient and by using another constant for the ions transported to the cell wall for a given value of pressure gradient acting for a given time. The equations representing the course of the changes of concentration with time are linear, and therefore in the beating situation we can assume a steady pressure gradient on which is superimposed a sinusoidal pressure variation. The equations then apply separately to the two kinds of pressure gradient.

We now find that for sinusoidal pressure variations the magnitude of the concentration changes at the cell wall and hence the size of the excitation is inversely proportional to the square root of the rate of the pressure variations. If the beat rate is represented by γ , then the size of the just-noticeable amplitude change ΔJ is given by the equation $\Delta J = K/\sqrt{\gamma}$, where K is a constant. This formula holds only for a limited region of frequency, because for very slow beats the well-known adaptive processes of the nerves arise, and the assumption that the fluid material transported through the cell wall is proportional to the pressure no longer holds. Long-continued pressures bring about a state of equilibrium in which there is no longer any fluid flow and the proportionality to time disappears. On the other hand, the size of the amplitude change cannot be greater than the amplitude of the tone on which the beating is imposed, and here also the formula encounters a limitation.

To test these considerations the circuit of Fig. 7-29 was used. The frequency of the oscillator G_2 was set so as to give four beats per second with oscillator G_1 , a rate that is most clearly observable. Attenuator b_1 was used to produce an intensity of 40 db above threshold, and attenuator b_2 was adjusted to give just-perceptible beats when the tone pulse was presented by means of the automatic switch. For the second presenta-

tion the frequency of G_2 was raised, and hence the beat rate was increased by the amount determined by the condenser C . Thereupon the change of amplitude had to be increased by manipulating attenuator b_3 so that the superimposed tone was greater relative to the tone delivered earlier through b_2 . The increase that was necessary to keep the beating audible

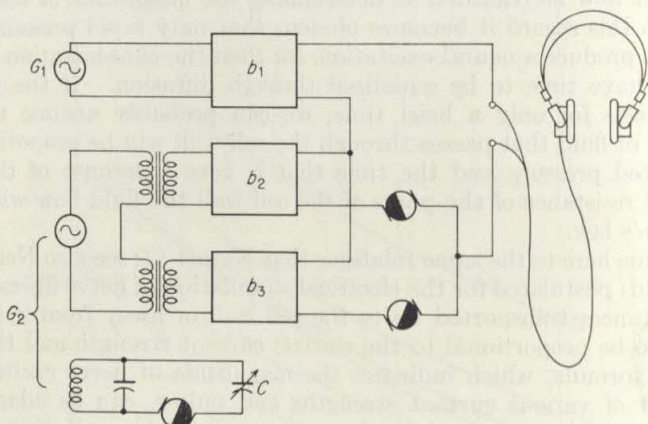


FIG. 7-29. Circuit for determining the audibility of beats of different rates.

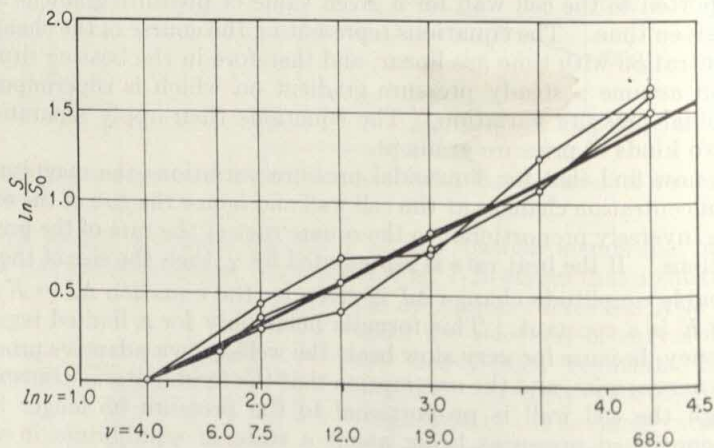


FIG. 7-30. The relation between rate and amplitude of beats. The solid line represents the calculated curve. $\ln \nu$ represents the natural logarithm of the rate of beating.

after the beating rate was increased is shown in Fig. 7-30. Here the heavy line represents results calculated from the formula, and it is clear that they are in good agreement with the measurements down to a low beat rate of four per second. Also the preliminary observations that Riesz carried out to determine the most suitable beat rate for his measurements are in agreement with the formula, as shown by the constancy of the numbers in the last column of Table 7-2. In the second column of

this table is shown the relative amplitude of the superimposed tone that is necessary to give audible beats.

TABLE 7-2

ν	A_2/A_1	$\frac{A_2/A_1}{\sqrt{\nu}} \times 10^2$
4.0	0.056	2.8
9.0	0.0825	2.75
17.0	0.117	2.84
35.0	0.149	2.52

If two equally loud tones are presented to the same ear they produce beats. If the beat rate is slow, it is possible to follow the rise of loudness to its double value, and then its fall to nearly zero. But if the beat rate is larger, the changes of concentration at the cell wall do not any longer

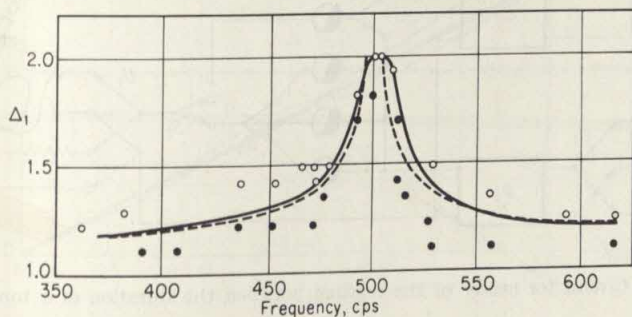


FIG. 7-31. The loudness of two beating tones at their maximum as a function of the beating rate. One of the tones was maintained at 500 cps, and the other was varied as shown on the abscissa. The broken line represents a calculated curve.

follow the rapid changes of pressure, and therefore in the brief period of the beat they fail to attain the double value. Therefore a comparison of the maximum loudness produced by two tones of the same amplitude with a tone of constant amplitude shows that as the beat rate increases the maximum steadily grows smaller, until finally it can no longer be recognized. Then the loudness of the two beating tones is the same as for one of them. Up to $\nu = 4$ the loudness doubling is still present, and from here on the magnitude of the beating tone decreases as the square root of the beating rate, as indicated above. Hence the maximum loudness is represented by the formula $(1 + \sqrt{4.0/\nu})L_0$. A comparison of observed results and loudness calculations from this formula is afforded by Fig. 7-31. The ordinate represents the loudness increase relative to one of the two equally loud tones. The solid line represents the observations and the broken line the calculated curve. Considering the difficulty of the observations, the agreement is excellent. Similar results were obtained for 200 and 2000 cps, and showed that the decrease of

loudness does not depend on the percentage change of frequency, but merely on the frequency difference between the two beating tones.

The fact that the neural excitation becomes smaller as the frequency of the pressure variations becomes greater strongly suggests that in the usual excitation of the nerve endings of the basilar membrane, brought about by the periodic flexing of the membrane due to a steady pressure of eddies in the fluid, the main portion of the excitation is to be ascribed to the steady pressure. This situation contributes to the fact that the excitatory characteristics of the nerve endings are the same for all tones.*

Nernst's formula further indicates that the introduction of a constant current i for the time t at the cell wall produces a change of concentration $C_0 - C = Ki\sqrt{t}$. Therefore the loudness of a tone pulse depends upon its duration, or $L = K\sqrt{t}$. To test this relationship the circuit of

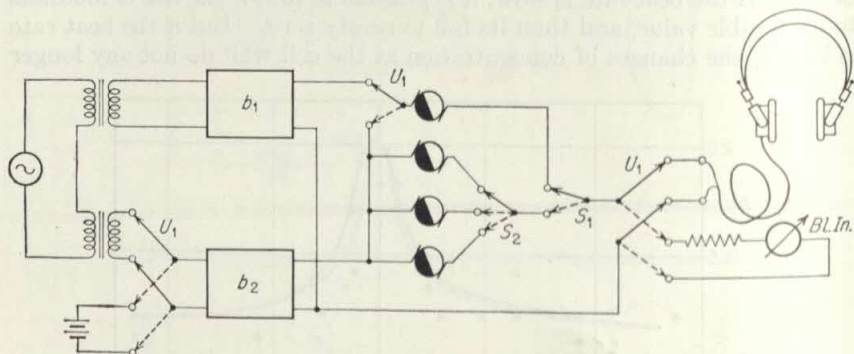


FIG. 7-32. Circuit for study of the relation between the duration of a tone and its loudness.

Fig. 7-32 was used, with a tone of 800 cps at 40 db above threshold. When the switches marked U_1 were in the uppermost position they were all automatically coupled. Switch S_1 likewise was set at the upper position, and then the uppermost interrupter, which rotated continuously, delivered a tone pulse of 0.1 sec duration to the phone. The loudness of this pulse was controlled by attenuator b_1 and was compared with that of a shorter pulse by setting S_1 to the lower position and adjusting attenuator b_1 . Switch S_2 permitted a selection of various pulse durations by the rotating interrupter. It was necessary to measure the durations of the pulses because they were readily altered by poor contacts. These durations were measured by switching U_1 to its lower position, so that a constant direct current was imposed on b_2 . If the rotating inter-

* [These conclusions concerning the importance of static pressure in hearing were made in 1929. Later experiments with enlarged models of the cochlea and the skin as a nerve supply seem to indicate that the steady pressure is not necessary and that the phenomena produced on the skin are closely similar to those in hearing. Unfortunately the experimental efforts to determine whether the vibrations undergo rectification have been inconclusive both for hearing and for skin stimulation. This question has to be kept open until more is learned about the electric discharges of both auditory and skin nerves.]

rupter was set so that only one pulse followed the pressing of a button, a momentary current was produced that could be measured on the ballistic meter whose resistance was matched to that of the attenuator. To determine the duration of the various pulses, b_2 was set for each interrupter so that the instrument always showed the same deflection. Then the differences in the settings of the attenuator represented directly the natural logarithm of the durations. The use of an attenuator as a shunt for a ballistic instrument is always to be recommended if sufficient energy is available for the attenuator to be set to a large enough value that the resistance of the current source cannot have any effect upon the attenuation. If an ordinary phone is used for the measurements, its damping should be increased artificially, for otherwise the brief pulses will produce

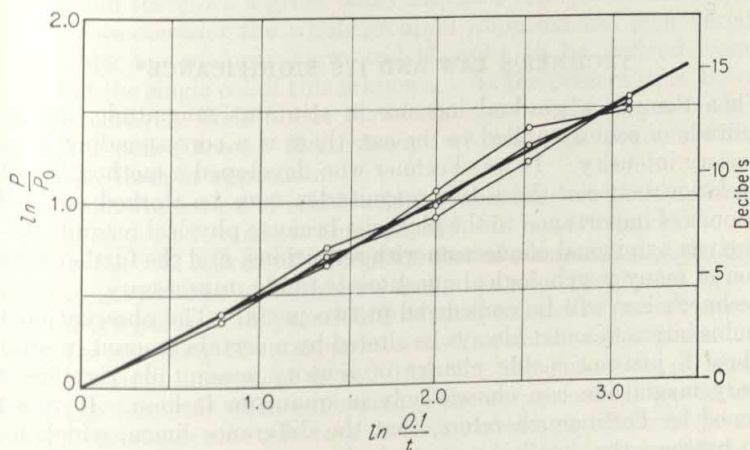


FIG. 7-33. The effect of duration upon loudness for 800 cps at 40 db above threshold. The abscissa represents the duration of the tone pulse (expressed as the natural logarithm of the fraction $0.1/t$) and the ordinate represents the sound pressure relative to that at 0.1 sec (also expressed logarithmically).

distortion. The increases in sound intensity necessary with brief durations of tone to give loudnesses equal to those of a comparison tone of 0.1 sec are represented in Fig. 7-33, together with values calculated by means of the formula (heavy curve).

For brief durations of the pulses the tone passed over into a dull click, and the same thing was found for low tones, namely, that a given increase in the intensity of the click produced a greater change of loudness than this increase in the 800-cps pulse. Up to 40 db above threshold these variations are not observable. Results for greater loudnesses are given in Table 7-3, which shows in the first row the amount of increase in sound pressure required for a pulse of 0.01 sec duration that was equal in loudness to the indicated increase in sound pressure for a pulse of 0.1 sec duration.

These results show that, for intensities above the 40-db level, the shortening of the tone pulse brings out more and more the click character

TABLE 7-3

Duration of pulse, sec	Equivalent increase in sound pressure, db			
0.01	40	60	80	100
0.1	40	57.6	75.7	94.8

of the tone pulses, and therefore the loudness does not decrease as rapidly as the formula indicates. As the tone is transformed into a click its loudness is increased. These observations confirm other measurements (page 358) of the increase in the loudness of a tone of 10 dynes per sq cm as a function of its duration.

FECHNER'S LAW AND ITS SIGNIFICANCE*

When there is a gradual increase in stimulus magnitude, as in the magnitude of sound applied to the ear, there is a corresponding increase in sensory intensity. It was Fechner who developed a method by which the relation between these two magnitudes may be worked out. This relation is of importance to the physicist because physical magnitudes are then given a univocal connection with sensations, and the further investigation of many psychological questions is made unnecessary.

Fechner's law will be considered in two parts. The observation that stimulus intensity must always be altered by a certain amount in order to produce a just-noticeable change of sensory magnitude signifies that sensory magnitude can change only in quantum fashion. It was first assumed by Fechner, therefore, that the difference limen, which is the ratio between the smallest quantum of sensation and its corresponding stimulus variation, is determined by the structures of the nervous system and cannot be reduced by an effort of attention or by practice.

In the second place, it was assumed that the quantum steps of sensation are equal in magnitude throughout the whole sensory range.

If these two statements are valid, then any increase of stimulus intensity beyond the difference limen will give a corresponding increase of sensory magnitude, and the relation between these two supraliminal magnitudes can be obtained, because the sensory magnitude is proportional to the number of just-noticeable differences into which the given stimulus intensity can be divided.

The correctness of the relation obtained in this way between stimulus intensity and sensory intensity cannot ordinarily be subjected to exact test, because a sensory intensity, such as loudness, is not scaled and its changes can only be estimated in a crude manner. In directional hearing, however, the shifting of the sound image out of the median plane presents us with a sensory quantity that is directly measurable in centimeters (see page 284). Here, therefore, the relation can readily be tested.

* Article 6 as listed in the Author's Bibliography. Published in 1930.

According to the first statement it is possible to derive relations concerning the size of the error of observation in loudness comparisons, and according to the second statement it is possible to discover the dependence of the difference limen for loudness on sound intensity. Also Fechner's law can be tested in this process.

Error of Observation as Dependent upon the Quantum Character of Sensory Magnitude. The laws of nerve action can be presented in two ways, one macroscopic and the other microscopic. The microscopic presentation begins with the fact that during stimulation the individual nerve cells respond with brief electrical potentials of practically constant amplitude, while the rate of these impulses increases with the stimulus intensity. Every stimulus involves a number of nerve cells at any moment, and therefore a great many impulses follow one another in the series. If we consider the whole group of impulses and their variations we have the macroscopic view, which ought to be derived from the behavior of the single cell if this is known. At the present time, however, we know relatively little about the interactions of the various cells that make up a nerve tract. Accordingly, we must be content with the macroscopic form of approach.

For the determination of relationships of this kind we must make use of particular ideas and concepts that certainly do not correspond to actual conditions but still represent a large number of phenomena of the macroscopic category. The situation is similar to one in physics in which representing a gas as a compressible fluid gives a series of correct principles without the necessity of entering into the kinetic theory of gases.

The following conception is set forth for the sensation of loudness produced by a sound. The excitation of the nerve endings on the basilar membrane produces an excitatory current whose magnitude may vary in a manner that initially is unknown, because it depends upon conditions of fatigue and the like. The excitatory current is increasingly effective in its action on the various cells along the basilar membrane from which the sensations of loudness arise. Then if a new cell is stimulated there is an increase in loudness, and the difference limen is explained. Because the nerve cells are much alike it seems clear from an anatomical standpoint that the loudness of a sound increases by a particular amount whenever a new cell is added, regardless of the number of cells already in action. The two Fechnerian laws can be derived from this picture.

The acoustic situation, especially with regard to loudness, differs from that of the other senses, such as vision, in that the difference limen is particularly large. Thus in visual measurements the various errors arising in the optical equipment are of the order of magnitude of the difference limen, and it can be assumed that the error of observation is a composite of many small unrelated errors in accordance with the Gaussian law. In acoustic measurements, however, this assumption is not permissible because here the error of observation is determined solely by the difference limen. In general, the physical magnitudes given by the acoustic apparatus can be determined with greater precision than the difference limen, which for loudness is of the order of 5 per cent.

Consequently the error function for loudness measurements can be determined from the quantumlike variations of sensation. Consider in this relation a comparison of the loudness of two successive tone pulses.

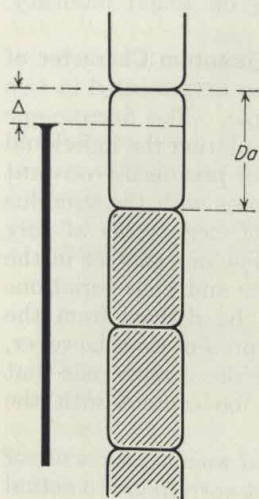


FIG. 7-34. The quantum character of excitation. A change of Δ or $D_a - \Delta$ does not affect the loudness, because the number of excited cells is unaltered.

If the excitation produced by these two stimuli is the same, there will be the same number of stimulated cells. If the excitation changes in magnitude, as indicated in Fig. 7-34, the sensory magnitude will be altered, provided that the change is sufficient to involve one cell more or one cell less. If a given stimulus always produces the same excitation, then, as the figure shows, the excitation can be increased by Δ or decreased by $D_a - \Delta$ without any alteration in the number of stimulated cells. Here are two values of stimulus for which the loudness remains the same.

If loudness comparisons are carried out by the method of constant stimuli (see above, page 211), results like those of Fig. 7-35 are obtained. Here one stimulus was kept constant and others were varied from it by certain amounts as indicated on the abscissa. The ordinate shows the percentage of judgments of equality of loudness. It is clear that in a certain region these judgments ought to be 100 per cent, and outside this region 0 per cent, giving a rectangular curve as indicated by the dotted line. However, the actual curve as shown, which was obtained with a tone of 300 cps at 40 db above threshold and an interval between pulses of 2.0 sec, departs markedly from the ideal function.

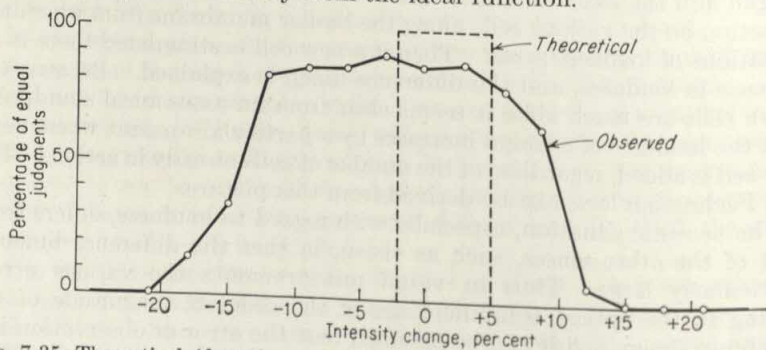


FIG. 7-35. Theoretical (dotted rectangle) and actual distribution of equal judgments as a function of the difference of intensity between standard and comparison stimuli. The standard was 300 cps at 40 db above threshold.

It is first to be noted that at no point does the actual curve reach 100 per cent. This happens because the excitation produced by a given stimulus is subject to considerable alteration from time to time. Such

alterations result from a sinking of the persisting trace as conceived by Köhler (3) through temporally varying fatigue, or other things such as variations of the ever-present sound of the circulatory pulse in many persons.

All the disturbances cause the magnitude of the excitatory difference between two successive stimuli to be increased or decreased in an irregular manner, and therefore the steep course of the rectangular curve is flattened out. If the variations of the excitatory change are larger than the difference limen, there will often be perceptible changes in loudness that should not otherwise appear, and the number of equal judgments will fall below 100 per cent.

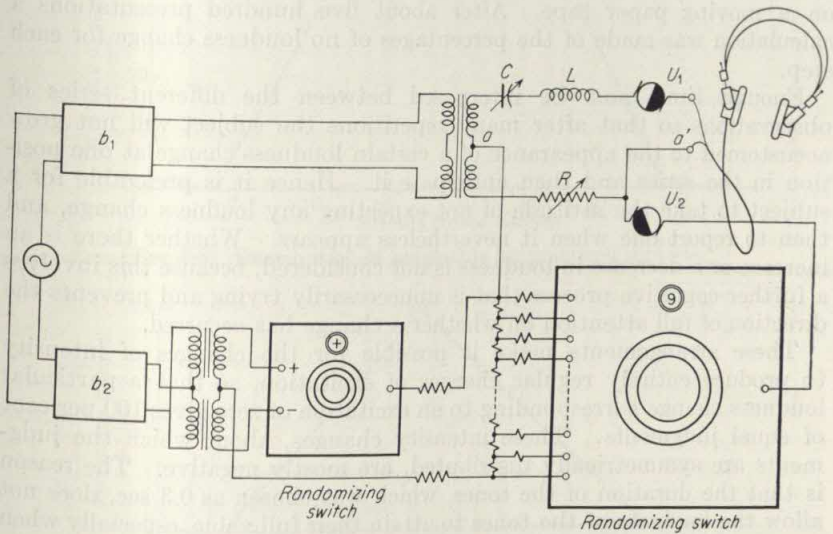


FIG. 7-36. Circuit for presenting pulses in immediate succession.

To avoid these temporal variations, the tone pulses to be compared can be presented in immediate succession. The circuit used for this purpose is shown in Fig. 7-36. A phone was placed in a bridge circuit so that when switch U_1 was closed the phone current was controlled by attenuator b_1 . If a little later U_2 also was closed, this current was increased or decreased according to the phase of the current in b_2 . Then later, when U_1 was opened, the phone current was stopped. For moderate loudnesses the duration of the tone was chosen as 0.3 sec. The duration of the second tone of a different intensity was also 0.3 sec. The transient arising when U_2 was switched in, which varies with the size of the change in intensity, was filtered out by placing the phone in a resonant circuit. This circuit was tuned to the frequency of the tone so that its effective resistance in the bridge circuit, together with that of the phone, was balanced by the resistance R . This balancing was done by switching off U_2 and placing a second phone at points a and a' , and then adjusting for

a minimum of tone. Then when the damping was sufficiently great in the attenuators their two currents could be superimposed in the phone without transients.

The various changes of sound intensity could be presented by means of a potentiometer and a randomizing switch, as already described (page 212). This procedure ensures an exploration of the extreme ends of the error curve.

The two switches U_1 and U_2 were operated automatically after a button was pressed. When it was ascertained that there was a change of loudness during the presentation of the tone, the two randomizing switches were advanced a step further, and then a reading was taken of the magnitude and direction of the observation. The data were recorded on a moving paper tape. After about five hundred presentations a calculation was made of the percentages of no loudness change for each step.

Enough time must be interposed between the different series of observations so that after many repetitions the subject will not grow accustomed to the appearance of a certain loudness change at one position in the series and then anticipate it. Hence it is preferable for a subject to take the attitude of not expecting any loudness change, and then to report one when it nevertheless appears. Whether there is an increase or a decrease in loudness is not considered, because this involves a further cognitive process that is unnecessarily trying and prevents the direction of full attention on whether a change has occurred.

These arrangements make it possible for the changes of intensity to produce entirely regular charges of excitation, so that a particular loudness change corresponding to an excitation of zero gives 100 per cent of equal judgments. These intensity changes, about which the judgments are symmetrically distributed, are mostly negative. The reason is that the duration of the tones, which was chosen as 0.3 sec, does not allow the loudness of the tones to attain their full value, especially when the tones are weak. Thus the loudness tends to be perceived as remaining constant rather than as increasing. This effect would be larger with still briefer tones.

Though it seems reasonable to assume that a particular change of excitation always corresponds to a given loudness change, it nevertheless is found that even though the first tone pulse was kept at a constant intensity there was a continual change in the absolute magnitude of the excitation from one comparison to another.

Therefore, as Fig. 7-34 shows, an increase in excitation of Δ was not always sufficient, for the amount necessary to give a loudness change varied with the level of excitation and might even be less than Δ if the level at the moment was at the upper end of a cell.

If we assume that the excitation level $D_a - \Delta$ can take all possible values with equal probability, then an increase of excitation of Δ will give a number of judgments of no change that is proportional to $D_a - \Delta$, and a number of possible judgments proportional to D_a . Hence the probability that an excitation change of Δ will not alter the apparent

equality of loudness is $w = 1 - \Delta/D_a$. Here the absolute value of Δ lies between the limits $0 < |\Delta| < D_a$.

If $\Delta > D_a$, there will always be an increase in loudness, so that for this condition the probability will always be zero. The same considerations hold for negative values of excitation, for then the sign of D_a is simply reversed. Thus instead of the rectangle of Fig. 7-35 we obtain for the error curve a triangle whose apex is at 0 and that attains a value of 100 per cent at $w = 1$, while the base of the triangle has a length on the abscissa of two difference limens.

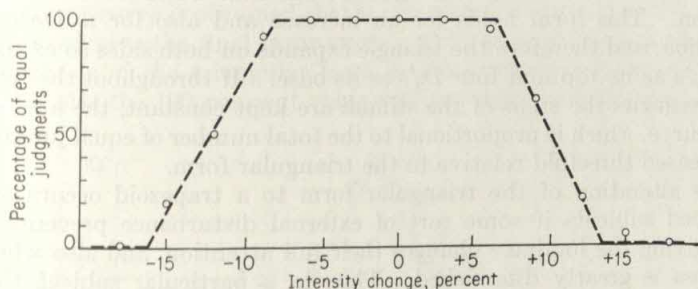


FIG. 7-37. Distribution of judgments for practiced subjects.

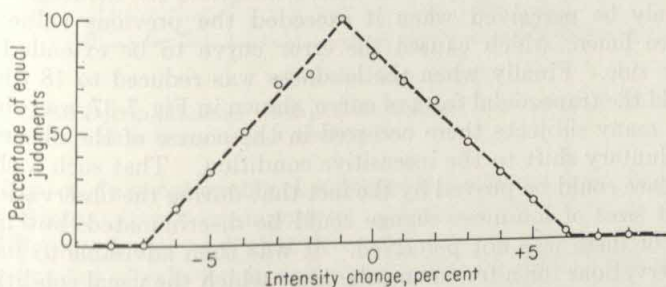


FIG. 7-38. Distribution of judgments for certain highly practiced subjects.

The experiments showed that with unpracticed subjects the error curve at the beginning included large variations from time to time. After a fair amount of practice, however, the results became fully reproducible and adhered closely to the form shown in Fig. 7-37.

After further practice of about a month some of the subjects gave a curve like that of Fig. 7-38, which agrees with the calculations.

We might suppose that an error curve like that of Fig. 7-37 arises because in the various observations the variations in the absolute magnitude of the excitation are smaller than the difference limen and so remain in the middle part of the rectangular form of the error curve. However, this is not the case. When the loudness was made so great that the difference limen always remained constant, as it does at 40 db above threshold, it was possible to vary the voltage of the oscillator of Fig. 7-36 up and down in an irregular manner about the original value, and by

amounts larger than the difference limen, without producing any alteration in the form of the error curve. Yet this procedure must have caused large variations in the magnitude.

The curve of error is based upon the fact that in subjects that are not well practiced the excitation must involve at least two additional cells before any change is perceived. They do not experience any alteration of loudness when the change is smaller than the difference limen. Therefore the probability remains constant at 100 per cent, and then when the change has a value between one difference limen and double this amount the error curve falls along a straight line like that found for the triangular function. This form holds for an increase and also for a decrease of excitation, and therefore the triangle expands on both sides so as to have two D_a 's as its top and four D_a 's as its base. If throughout the series of measurements the steps of the stimuli are kept constant, the area of the error curve, which is proportional to the total number of equal judgments, is increased threefold relative to the triangular form.

This alteration of the triangular form to a trapezoid occurs also in practiced subjects if some sort of external disturbance prevents them from giving the loudness changes their full attention, and also when the loudness is greatly diminished. Thus in a particular subject the triangular form was maintained when the loudness was dropped to 22 db above threshold, whereas at 20 db above threshold the loudness decrease could only be perceived when it exceeded the previous value of the difference limen, which caused the error curve to be extended on its negative side. Finally when the loudness was reduced to 18 db above threshold the trapezoidal form of curve, shown in Fig. 7-37, was obtained.

With many subjects there occurred in the course of the observations an involuntary shift to the insensitive condition. That such a shift has taken place could be proved by the fact that during the observations two different sizes of loudness change could be discriminated, but now the smaller of these was not perceived. It was then advisable to interrupt the observations for a few moments, after which the usual condition was restored.

Ordinarily an attempt was made to increase the precision of the measurements by repeating every observation at least twice and recording the judgment only if equality was perceived both times. If w is the probability that a difference of sound intensity Δ will not be perceived as a loudness difference, then the probability that this observation will be made twice is w^2 . Then the error curve for a practiced subject will give

$$w = \left(\frac{\Delta}{D_a} \right)^2 \quad (7-1)$$

In Fig. 7-39 the broken curve shows the calculated values and the points represent the observations. At the same time the number of equal judgments declined to two-thirds, so that the repetition of observations gave a material improvement in the precision. For some subjects, however, for whom the curve of error had a trapezoidal form, there was

no reduction of the number of equal judgments in the middle region even when the observations were repeated. For them there was a variation only at the edges of the trapezoid, where there was a steep drop instead of a straight line, as Eq. (7-1) indicates. For these subjects, therefore, this procedure did not improve the precision to any significant degree.

If a loudness comparison between two tones is carried out by switching from one tone to a second and then back to the first, it is necessary to consider that along with the reversal of the order of the comparison there is a reversal of the direction of the shifting of the error curve from the mid-line $\Delta = 0$, as shown in Fig. 7-38, so that for each half of the observations an error curve is obtained that is symmetrical about $\Delta = 0$. These two together give the final error curve. It is then clear that when the error curve is of the triangular form it is considerably flattened at its apex, and also the 100 per cent value will no longer be obtained.

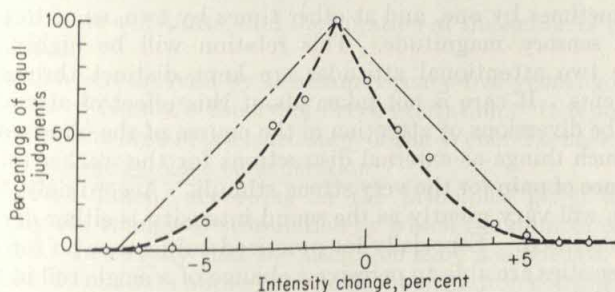


FIG. 7-39. Distribution obtained when the requirement is made that two successive judgments of the same stimulus pair must agree.

Equality of Just-noticeable Loudness Differences over the Entire Sensory Scale. It is now important to establish that it is not the size of the difference limen itself that determines the magnitude of sensation, but the number of cells set in excitation. Thus a shift of attention, as might be produced by a preliminary signal of a different sort from the usual one, can produce a significant increase in the size of the difference limen. This can happen even when there is no alteration in the perceived loudness. If the loudness were proportional to the number of D_a 's into which the intensity of the tone can be divided, then there ought to be an alteration in the loudness at the same time.

To study this point further, a battery was placed in series with the phone of Fig. 7-36 so that when a switch U_1 was closed a click was produced, making the loudness changes more difficult to observe. It can clearly be noted as the disturbing noise is made stronger that a subject with the triangular form of error curve fails to perceive the smallest changes of loudness and reports only the larger ones, though the weaker clicks do not produce any variations in the loudness of these tones.

Also, if loudness was determined directly by the difference limen, the threshold stimulus would always seem of the same loudness, for as the intensity is increased the threshold is always the first D_a . It is well

known, however, that in a completely quiet room where the subject can only hear his own pulse, it is possible to observe changes in the loudness of the threshold stimulus as time goes on, for weaker and weaker tones come to be perceptible.

Often there is no alteration in the character of a tone as the threshold is approached. Then the sensation of pitch vanishes simultaneously with the sensation of loudness. Under certain conditions, however, as with enhanced attentiveness, the threshold of intensity lies considerably below the threshold of pitch. Then there is no true perception of sound, but only an impression that a stimulus is present.

Therefore it seems likely that at the threshold a number of cells are in action, and this number can be reduced only by a special intensification of attention.

On the assumption that the difference limen depends upon the sound intensity, it can be supposed that the number of excited cells must be altered sometimes by one, and at other times by two, so as to produce a change in sensory magnitude. This relation will be highly irregular unless the two attentional attitudes are kept distinct throughout the measurements. If care is not taken about this effect of attention, then there can be diversions of attention in the course of the observations as a result of such things as external distractions for the weaker stimuli and the incidence of pain for the very strong stimuli. Accordingly, the difference limen will vary greatly as the sound intensity is either decreased or strongly increased. Especially for practiced subjects, who for moderate sound intensities are able to perceive a change of a single cell in the group stimulated, these variations are common. For the unpracticed subject, who requires changes of at least two cells, the attentional set remains constant over most of the intensity region.

From these considerations it is at once apparent that Fechner's second law holds true only in the region of intensity where attention does not change. Hence the difference limen always represents a constant change in the number of excited cells. The failure to appreciate this limitation is responsible for the many divergent opinions expressed in the literature about the validity of Fechner's law. In order to demonstrate the serviceability of this law, the dependence of the difference limen for intensity upon sound intensity will be worked out.

It is well known that the maximum pressure gradient operating on the nerve endings of the basilar membrane through the action of a sound is proportional to the sound pressure. Hence, according to the theory of nerve excitation (page 232), the changes of concentration at the cell wall are likewise proportional to the pressure, provided that the sound action is not too prolonged. Lehmann is to be credited with the valuable suggestion that according to electrolytic theory the changes of concentration give rise to a potential difference that excites the nerve fibers. The magnitude of the excitation increases with nearly constant amplitude so that a number of cells are excited in proportion to the stimulus intensity and hence also the potential difference. Thus according to the results obtained on the increase of loudness caused by the simultaneous presenta-

tion of two tones of different frequency, the sensory magnitude along the basilar membrane is determined by the maximum value of the potential difference.

Let us represent the sound pressure by J and use aJ to represent the increase in concentration arising at a region of the cell wall as a result of a pressure gradient. Then aJ can be used as a measure of sensory magnitude. Let c be the concentration preceding the action of the sound, which will remain constant over the greater portion of the cell wall for tones of brief duration. Then the potential difference arising between the two portions of the cell wall, according to the theory of concentration series, is given by the logarithm of the concentration ratio $(c + aJ)/c$. Then the excitation is given by

$$E = b \log_e \left(1 + \frac{aJ}{c} \right) \quad (7-2)$$

where b and a/c are constants, and the duration of the action of the sound is kept constant.

This equation was derived by Lehmann twenty-five years ago without any knowledge of Nernst's theory of nerve excitation. It represents at the present time the best-established form of the Weber-Fechner law, and will be given especially close consideration.

The difference limen, according to the principles given above, is determined by the change of stimulation by which the number of excited cells is altered. Let us say that the alteration is by a single cell. Beginning at a point 10 or 12 db above threshold, this situation corresponds to a constant excitatory change of ΔE , and the corresponding change of intensity $\Delta J/J$ can be calculated from Eq. (7-2).

For two successive clicks, Lehmann has already calculated the threshold as obtained by the method of limits. According to this method, the second click is made larger until it clearly appears louder. Because under these conditions the sinking of the trace of the first click plays an important role, it is necessary to derive a special theory for the sinking in order to be able to calculate the difference limen.

This serious complication can be avoided if the difference limen is obtained by the method of constant stimuli or by the method used by Knudsen (1). Knudsen introduced amplitude variations into a continuous tone and enlarged these until they became perceptible. Under these conditions the sinking of the trace is of no importance, and Eq. (7-2) gives directly the value of the constant ΔE , as

$$\Delta E = b \log_e \frac{1 + \frac{a}{c} (J + \Delta J)}{1 + \frac{a}{c} J}$$

whereupon the equation gives $\Delta J/J = k_1 + k_2/J$, where k_1 and k_2 are constants. This equation requires that the duration of the variation of the tone be kept constant.

If J is small, *i.e.*, if the sound intensity is raised from zero until a difference in sensory magnitude is obtained, then ΔJ agrees with the auditory threshold J_0 , and we have $J_0 = k_2$. On the other hand, if J is significantly larger than threshold, then as J increases, the difference limen approaches a constant value that must be determined from the measurements, and then $\Delta I/I = k_1$. The difference limen therefore depends upon the stimulus intensity as indicated by the formula

$$\frac{\Delta J}{J} = \frac{\Delta I}{I} + \frac{J_0}{J}$$

The observed and calculated values of the difference limen reported by Knudsen (1) are given in Fig. 7-40. The threshold J_0 , which may be

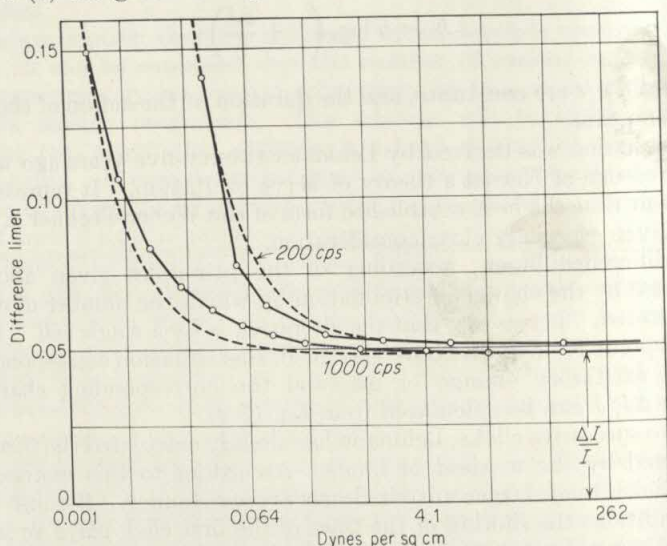


FIG. 7-40. Knudsen's results on the difference limen for intensity as a function of sound pressure. The dotted curves are calculated.

called the "absolute threshold," was calculated from the point to the extreme left, and its intensity was found to be 19 db below the observed point for a tone of 1000 cps. A direct measurement of the normal threshold gave a value 6 db below the observed point as shown on the extreme left. If in the determinations of the difference limen the strength of excitation is altered by just one cell, it appears that at the normal threshold there is an excitation of about five cells.

If we consider that the curve is drawn on the basis of only two points of observation, then the agreement between the calculated and measured values is a good confirmation of the theory. Note in this connection that the variations for 1000 and 200 cps are in opposite directions and are still smaller for a third series of measurements that have not been shown. Also a small part of the variation is to be ascribed to the nonlinearity of the ear.

the vibratory body K , which was supported in the proper position on the skin by a number of thin rubber bands. When the finger tip was placed on the plate P , it was only necessary to adjust the attenuators b_1 and b_2 in order to obtain equal intensities of the successive pulses of vibration and tone. By the method of limits the measurements were repeatable within 30 per cent, and it was possible to show that equally intense pulses of vibration and tone are still perceived as equal if both are changed in amplitude by the same factor. It follows that the excitatory processes are the same for the two senses.

Fechner's Law in Directional Hearing. Two successive clicks were found to be unsuitable for determination of the locus of the sound image along the rectilinear pathway (see below, page 279). This was true because at the beginning of the observations there was always a certain direction or bias to the attention, and so there was a shifting in the

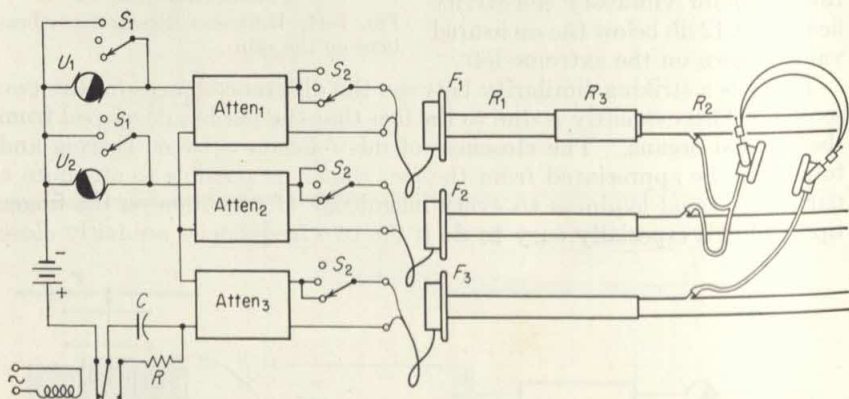


FIG. 7-43. Arrangement for determining the thresholds of displacement of a sound image.

position of the first image of the click on account of wandering of the attention. It was more satisfactory to use a rapid series of clicks or a noise lasting about 0.2 sec, which suddenly changed its direction, remained for 0.2 sec, and then disappeared. A suitable circuit for this study is shown in Fig. 7-43.

The series of clicks was presented by means of a 50-cps interrupter which charged a condenser C through the attenuators and discharged through the resistance R . The automatic switches U_1 and U_2 first actuated phones F_1 and F_3 and immediately thereafter F_2 and F_3 . As F_1 and F_2 had different tube lengths, there appeared a displacement of the sound image. Switches S_1 and S_2 served to give the correct polarity of the speakers and an equality of loudness for right and left ears, which it was necessary to maintain for both sound images.

The arrangement shown in Fig. 7-44 was used for fine adjustments of the tube length of F_1 without knowledge on the part of the subject. Tube R_1 was made to slide over R_2 . R_1 terminated at one end in the phone F_1 and bore at the other end a wooden cylinder on whose surface

were a number of projections variously placed. If R_1 was displaced to the left, one of the projections struck the stop G and prevented R_1 from moving any farther. Thus the tube lengths to which R_1 and R could be adjusted were determined by the position along the cylinder at which the projection was located. In this way various time differences were obtained.

The observations were made by shifting tube R_1 all the way to the left, observing the displacement of the sound image by operating interrupter U_1 , and then pulling R_1 all the way to the right and rotating one notch so that the tube length that had been used could be read on the scale. This length was recorded along with the observed displacement of the image. When R_1 was returned to its left position, the next projection came against the stop, and a further observation could be made.

There is an important difference between the difference thresholds for directional hearing and for loudness. In the observation of the loudness

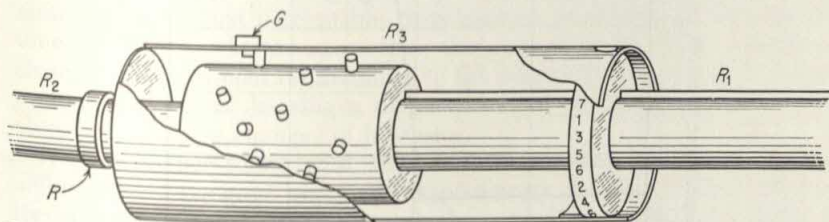


Fig. 7-44. Arrangement for varying tube length without knowledge by the subject.

changes between two successive tone pulses it was found on repetition of the observations that the magnitude of the tonal excitation underwent extensive variations from one time to another. Hence it seems that the excitatory changes take place in continually different groups of cells. These variations in the total magnitude of the excitation give to the error curve a triangular form. On the other hand, in certain subjects the just-noticeable displacements of the sound image indicate small variations in the time differences, due to variations over a period of time in the velocity of nerve conduction. Because a repetition of observations almost always brings in the same cells to the same degree, these results produce an error curve that approaches the ideal rectangular form.

It must also be considered that the difference limen in directional hearing is a function of the sharpness of the sound image. An image with distinct contours can exhibit much smaller displacements than one that is fuzzy at the edges. Here the same conditions operate as for the difference limen for tonal frequency.

A determination was made of the difference threshold for a displacement of the sound image from the mid-line along the rectilinear sound pathway. The course of the function is shown in Fig. 7-45 for a series of clicks whose intensity was 40 db above threshold. It is evident that the difference limen remains constant up to the first break point, and then beyond it rises suddenly to a value three times greater and maintains this value to the farthest position of the image. At first these observa-

tions were extremely difficult to carry out. They were disturbed by the fact that the small displacements could not be placed in a central position as is usual for sound sources in ordinary listening. Therefore as the displacements of the image went off center there was a slight increase in the magnitude of the difference limen. A few days of practice were sufficient to cause these effects to disappear and to permit the subjects to judge small displacements on one side of the head with the same accuracy as in the mid-line.

Because the sound image maintains its sharp contours over the whole extent of the rectilinear pathway, the results shown in Fig. 7-45 represent an excellent confirmation of Fechner's law. Actually the displacements of the image from the mid-line as observed are proportional to the time differences obtained by a summation of the constant difference limens.

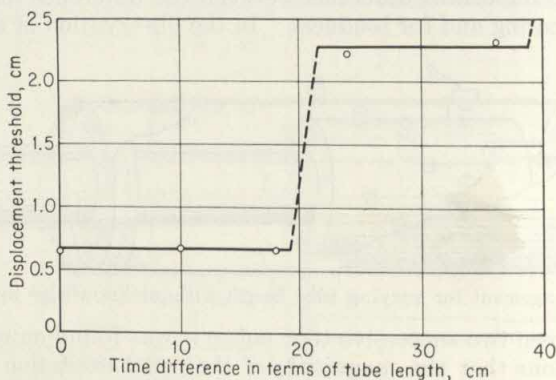


FIG. 7-45. Displacements of the sound image from the mid-line as a function of time differences.

As is well known, there is an unsteadiness in the displacements of the image when the time difference $\Delta t = k$, and the same is true for the difference limen.

It is further to be seen in Fig. 7-45 that for certain subjects a change in the time difference by 0.66 cm of tube length produced a change in the position of the image. This position from the mid-line up to the break point, where a time difference of 21.0 cm was attained, gave an extent over which $21.0/0.66 = 32$ spatially distinct image positions could be distinguished. From the break point up to the most lateral position there were 9 additional positions. Thus there were 80 anterior positions that could be recognized in response to a single noise.

The validity of Fechner's law for image displacements along the rectilinear pathway will again be investigated when the displacements are produced by unilateral variations of sound intensity. As will be shown, the displacements of the image from the mid-line are given by the equation

$$\frac{2\delta}{k} = (1 + c) \frac{S/s - 1}{S/s + 1} \quad (7-3)$$

This equation holds for those subjects for whom the Hornbostel-Wertheimer constant k varies but slightly with sound intensity. Here S/s is an increase of sound intensity in one ear following an equating of the loudness in the two ears, c is the constant of angular increase, and δ/k is the observed displacement relative to the displacement at the break point. If this equation is differentiated for S/s we obtain

$$d \frac{S}{s} = \frac{(S/s + 1)^2}{1 + c} \frac{\delta d}{k} \quad (7-4)$$

If on the right side of this equation we insert the values $c = 0.30$ and $\delta d/k = 0.63/22$, obtained as variations of time differences in the measurements of difference limens in a special case, then we obtain $S/s = 1$. Thus a sound image in the mid-line must have its intensity changed on one side by 8.7 per cent to give a displacement of the image that is of the same size as a just-perceptible displacement produced by varying the time difference. At the same time this subject could perceive loudness changes of 15 per cent on listening to the same sound in one ear. Moreover, in directional hearing a displacement of the image could only be observed for these changes of intensity.

It was further found that the smallest perceptible changes of time difference always gave an image displacement of about 3 mm, whereas the smallest perceptible unilateral changes of intensity gave displacements of about twice this amount.

Thus it is evident that a unilateral change in intensity giving a just-perceptible displacement of the image is not determined by the least-perceptible image displacement but rather is due to the fact that the auditory nerve fibers mediate only changes of sound intensity that attain the magnitude of the difference limen for loudness. Therefore these changes are considerably greater than the above equation indicates.

The difference limen for amplitude is larger than the formula indicates, not only in the mid portion of the sound pathway but also for the largest unilateral changes of intensity that have been considered here, which show as much as a fourfold increase or decrease over those in the mid-region. Thus along the entire rectilinear pathway the just-perceptible displacements of the image are determined by the difference limen for amplitude.

When sound intensities beyond 40 db above threshold were employed, this difference limen remained independent of intensity. Therefore a constant value, irrespective of the image position, was obtained for the percentage change of unilateral intensity for which there was a just-perceptible displacement along the rectilinear pathway. This value represents the difference limen for amplitude changes in listening with one ear. The data given in Table 7-4 show this relation with great exactness. The difference limen for amplitude was larger than usual because the two noise pulses that were being compared followed one another immediately.

TABLE 7-4

S/s	Necessary percentage change in S/s
Unilateral threshold	15.2
0.25	15.8
0.5	15.0
1.0	15.5
2.0	15.1
4.0	15.4

The results do not verify Eq. (7-4), despite the fact that Eq. (7-3) is correct for certain subjects. It seems, therefore, that Fechner's second law does not hold for an image displacement produced by a unilateral change of intensity. Also the image displacement cannot be regarded as a summation of difference limens. It is particularly clear that the nature of the image displacement for progressively larger unilateral changes of intensity is entirely different for subjects for whom the Hornbostel-Wertheimer constant holds than for other subjects for whom this constant varies with sound intensity. This is true even though the difference limen along the entire sound pathway remains constant and has the same value for these two classes of subjects.

Thus if Fechner's law is to be valid it is necessary that the excitation not be mediated by an intervening process representing a quantumlike rise in excitation for which the quanta are larger than the difference limen of the end organ. Then we could no longer suppose that the sensory magnitude increases an equal amount whenever the stimulation is increased by one difference limen.

Because the presence of one or more intervening processes is highly probable in a large number of sensory mechanisms, we cannot regard Fechner's law as universally valid.

Besides the displacement of the sound image along the rectilinear pathway, there are still other sensory effects whose magnitudes can be quantified. Examples are the impression of the distance of a sound source and the perception of the direction of a sound heard with one ear. For these it likewise may be shown that Fechner's law does not hold without modification.

Significance of Fechner's Law for Frequency Analysis. The logarithmic relation between a pressure stimulus and excitation brings about a significant reduction in the sharpness of stimulation along the basilar membrane in the region of resonance. Let us consider Helmholtz's resonance theory and calculate the damping of the cochlear resonators from the rapidity of trills, neglecting any action time of the nerve fibers. These results give a logarithmic decrement $\vartheta = 0.1$. A smaller value cannot be accepted, for then the transients of onset would be too large. In Fig. 7-46 the broken curve shows the vibratory amplitudes A corresponding to different degrees of tuning ω/ω_0 , expressed as ratios to the

amplitude of resonance A_0 . If we consider a tone whose intensity is 80 db above the absolute threshold, and thus for 100 cps is of about the level of normal speech, then Eq. (7-2) gives the distribution of excitation. This distribution is represented by the solid curve of Fig. 7-46 for E/k . Here it is assumed that on account of the spatial distribution of stimulation of the various nerve cells the concentration changes produced by the pressure gradient are independent of one another. Also the law of contrast operating for the various nerve fibers is left out of account. If the peak of this curve is taken as a resonance curve, then the logarithmic decrement must be more than six times larger than the value given above.

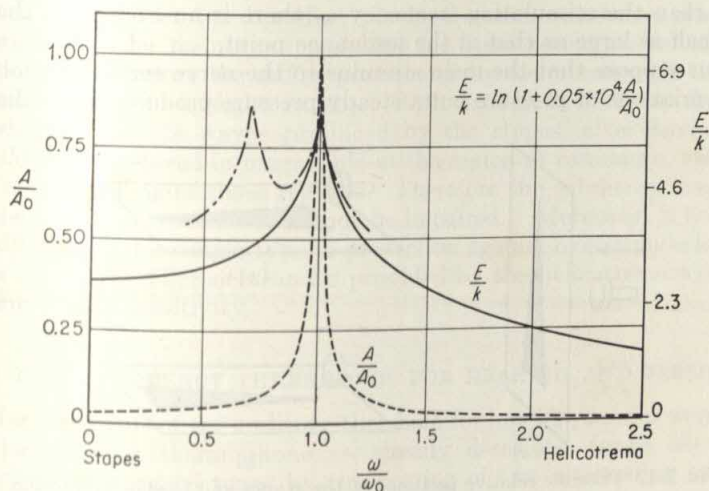


Fig. 7-46. Theoretical distribution of amplitudes along the basilar membrane according to the resonance theory of hearing. The dotted curve represents relative amplitudes for different degrees of tuning, when the logarithmic decrement is taken as 0.1. The solid line represents the logarithm of the vibratory amplitudes along the basilar membrane for the resonance theory.

If two tones are presented simultaneously with a frequency difference of 30 per cent, such as 1000 and 1300 cps, the maximum amplitude of vibration is the sum of the two amplitudes, as indicated in the figure by the broken curve.

It is obvious that even a damping of $\delta = 0.1$ for the cochlear resonators would not be small enough in consideration of the relations between stimulus and excitation, because the two tones when presented simultaneously seem like completely separate sensations, which would not be expected from the extensive overlapping of the excitation curves. Thus it is necessary for the Helmholtz resonance theory to resort to a contrast effect in its explanation of the resolving power of the ear. This is necessary inasmuch as a proportional relation between stimulus and excitation cannot be demonstrated, though such a relation is tacitly accepted in most considerations of auditory theory.

In the curves of Fig. 7-46 it was assumed that the pressure variations arising along the basilar membrane as a result of the movements of the stapes are constant over the entire extent of this membrane. The actual positions of the basilar membrane and the stapes are represented in Fig. 7-47*c*, and under these conditions the pressure variations are propagated up to the point of resonance of the membrane without appreciable loss. This is true because only at the resonance point and in the more lax regions beyond it is there any yielding of the membrane. Therefore a steeper decline appears only on the right side of the curve of Fig. 7-46. On the left side of the curve the regular form is maintained, so that even for a part of the membrane whose natural frequency ω_0 is considerably higher than the stimulating frequency ω , there is an excitation that is about half as large as that at the resonance point.

Let us suppose that the main stimulus to the nerve endings is not the rapid variations of pressure but a steady pressure produced by eddies in

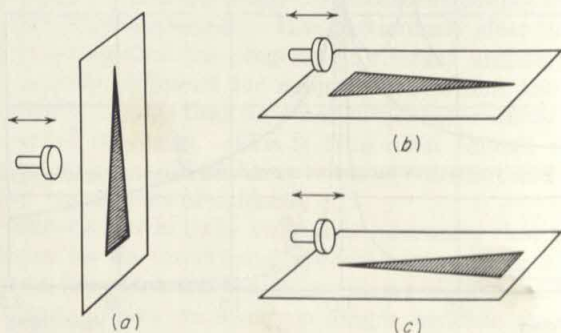


Fig. 7-47. Possible relative positions of the stapes and basilar membrane.

the fluid (see page 420). Then the eddies can produce considerably larger concentration changes in the nerve cells during the action of a tone than a sinusoidal pressure variation of the same maximum value, and hence provide more effective conditions. The eddy pressure extends only over an extremely narrow region of the basilar membrane and falls away to zero on both sides in symmetrical fashion. Hence the curve of excitation falls off steeply in the regions of the membrane that are tuned to the high frequencies, as is to be expected according to the Helmholtz theory.

Fatigue phenomena also are favorable to the eddy theory. The fatigue phenomena represent a neural process. Therefore we should expect from the results shown in Fig. 7-46 that a fatiguing of the ear by a continuous tone would not only bring about a weakening of the tone of the same frequency but also of higher tones. However, the observations did not support this expectation.

Still to be discussed in this connection is the fact that an excitation of the nerve endings by a steady eddy pressure rather than by pressure variations is likewise independent of the phase relations of the individual tones. Despite the relatively large viscosity provided by the cochlear duct, the different vibrations of the basilar membrane are simply additive

without distortion, and so also are the eddy movements that take place in the much less viscous fluid of the *scalae*. Accordingly, every tone can set up a pair of eddies in complete independence of others. Its eddies then combine with the eddies produced by another tone if the frequencies of the two tones are close together.

In this connection it should be mentioned further that among all the possible spatial arrangements between the stapes and the basilar membrane, the one that actually exists is the most effective for the stimulation of the organ of Corti, as may be seen in Fig. 7-47. The other two possibilities, shown as *a* and *b* in this figure, produce almost no pressure variations on the two sides of the basilar membrane, because the pressures are equalized over the broadest portions of the membrane where the elasticity of the membrane provides the least resistance to the fluid motions. Therefore the stiffer portions of the membrane will be set in vibration only to a slight extent. With arrangement *c*, on the other hand, the pressure waves produced by the stapes, after having been considerably reduced in magnitude at the region of resonance, will affect the more yielding of those regions. Therefore the vibratory magnitude at the region of resonance will not be impaired. Moreover, it is only in condition *c* that a simple type of protection against overstimulation by a direct pressure difference can be provided by the helicotrema without a serious loss of sensitivity.

LOW-FREQUENCY THRESHOLDS FOR HEARING AND FEELING*

Measurements of the auditory threshold for low frequencies were made by means of a thermophone as already described (page 66). This instrument produced tones by the beating of two alternating currents. The thermophone capsule was connected with a short tube, one end of which was sealed into the external auditory meatus by means of a rubber ring and petroleum jelly, and the other end of which was fitted with a membrane manometer. The thermophone and its electrical leads were made as light as possible so as to follow the movements of the head without setting up any extraneous pressures in the meatus. After the thermophone current had been adjusted to the threshold value, a biting board was used to keep the head in a fixed position. Then the sound amplitude could be determined by means of a light beam reflected from a mirror on the membrane of the manometer.

For the most part, a rubber membrane was used whose natural frequency and damping were measured by photographically recording the vibrations produced by a click. Hence the region of frequency was precisely known for which the static calibration of the membrane manometer could be continued to hold true. The sensitivity of the manometer could be raised sufficiently so that sound pressures could be measured directly at the eardrum for a 50-cps tone at threshold. For higher frequencies the sound pressure was measured with the manometer at greater intensities,

* Article 23 as listed in the Author's Bibliography. Published in 1936.

and then the thermophone current was reduced to whatever extent was necessary.

As a control, measurements were made also with a pump or pistonphone. A short T tube was connected to the ear, with one branch leading to the membrane manometer and the other branch connected through an acoustic filter to the pistonphone. The intensity was adjusted by a proper choice of the stroke of the piston and by varying a clamp on a cotton-filled rubber tube between the pistonphone and the filter. If mercury is used in the fluid filter as described earlier (page 60), a scum of oxide often forms on its surface after it stands for a time, and then a noise may be produced by its movements against the glass walls. This disturbance may be avoided by covering the mercury with a drop of alcohol.

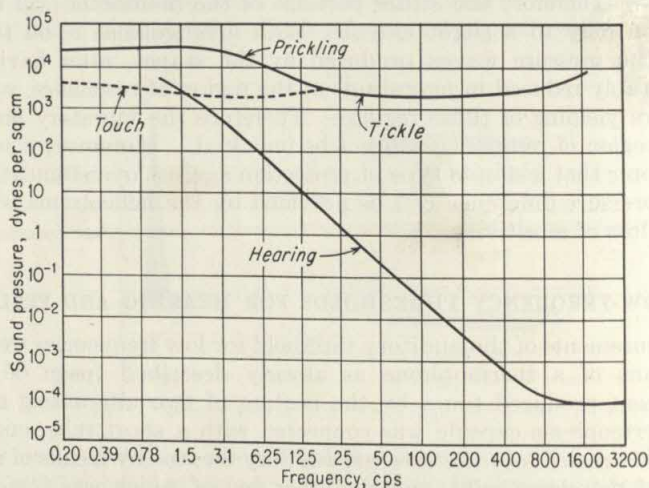


FIG. 7-48. Thresholds for various sensations aroused by low tones.

Results of threshold measurements on one ear are given by the lowermost curve of Fig. 7-48. The abscissa represents frequency and the ordinate the sound pressure at the eardrum. The values above 100 cps are taken from the observations made by Waetzmann (7) and Geffcken, and are in good agreement with the present measurements. Threshold measurements below 20 cps have been made by Brecher by means of a piston membrane driven by an eccentric. His results, as compared with those of Fig. 7-48, showed a somewhat more rapid increase in the threshold values as the frequency was reduced.

For frequencies above 20 cps the sensation in the region of the threshold was always one of a pure tone. When the frequency was reduced to 10 cps, however, the threshold stimulus in uniaural listening gave sensations of touch referred to the ear rather than sounds. In order to determine whether these touch sensations were mediated by the pressure nerves of the ear or by the auditory nerve, the phenomenon of directional

hearing was utilized. When two exactly symmetrical points on the skin of the head, as for example two points at the entrance to the external meatus, were stimulated simultaneously, it was difficult to fuse them into one. Instead, they were separately localized at the two ears. On the other hand, two auditory sensations were automatically fused to a single impression. If in one ear the 10-cps stimulus was held constant and in the other ear it was gradually increased from a low level, it was possible to observe first the masking of the tactual sensation in this ear, and then, as the loudness became equal in the two ears, the appearance of a pure auditory sensation which was localized in the mid-line of the head. Then when the loudness became unequal the sound was displaced toward one side. It is clear that at very low frequencies there is a close similarity between auditory and tactual sensations.

If the loudness in the two ears was kept equal and the stimulus magnitude was increased further, an effective pressure of about 2000 dynes per sq cm gave an auditory sensation in the mid-line of the head and also a tactual sensation in each ear. The tactual sensation in one ear was unaffected by variations of the stimulus in the other ear. It was truly a sensation of pressure. In Fig. 7-48 are shown the threshold values of these two kinds of sensation. For frequencies below 1 cps, as the intensity was raised from zero, the first sensation was one of touch, and only later did the auditory effect appear. Yet the directional phenomenon made it possible to separate these two and also to follow the tactual effect for a little way beyond its threshold.

For frequencies below 10 cps the slope of the threshold curve decreases, because when the sound pressures reach a magnitude of about 10,000 dynes per sq cm overtones arise in the middle ear and lower the threshold. It was possible to observe at times that these overtones are louder than the fundamental tone.

For frequencies extending all the way to 0 cps the tactual threshold continues to show only slight dependence upon frequency. If the ear was exposed to positive or negative pressure that was changed so slowly that a sensation arose only after 30 sec had elapsed from the onset of the change, a mean value was obtained for the touch threshold of 6000 dynes per sq cm. This value fits well into the curve of Fig. 7-48 when we bear in mind that the ordinate scale of this figure presents effective values. The range of the thresholds was 500 to 10,000 dynes per sq cm.

The tactual sensation produced in the ear by a steady air pressure bears a close resemblance to the sensation produced by touching the finger tip with a blunt object. Though a constant stimulus applied to the finger tip gives rapid adaptation (von Frey), a corresponding effect could not be demonstrated for the ear. When the air pressure applied to the external meatus was adjusted to a value that barely elicited a tactual sensation and was kept at this value, the sensation remained constant over several minutes. Also the feeling threshold that was obtained in this manner was not significantly changed when just before the test the ear was exposed for 2 min to a static pressure of 40 cm of water.

Careful examination revealed that the auditory threshold for low tones reflects the quantal character of neural processes. Thus if the frequency of the alternating pressures was changed slowly, and without any variation of magnitude, from 2 to about 50 cps, it was possible to observe that the loudness and the pitch did not vary continuously, but were altered in a steplike manner.

This discontinuity was most clearly perceptible in the region of 18 cps. As the higher frequencies were approached, there appeared a sudden increase in loudness, corresponding approximately to a doubling of the sound pressure. At the same time there was a doubling of pitch; the number of pulses, which were separately perceptible below 18 cps, suddenly became doubled, and the whole sensation became fused and

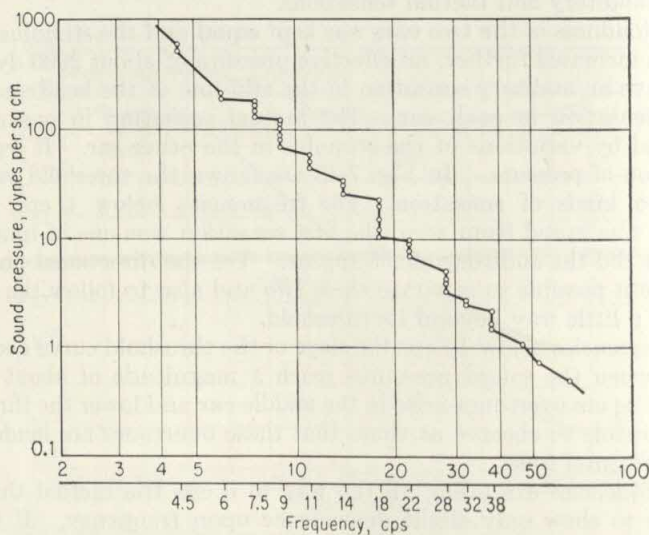


Fig. 7-49. Steplike form of the threshold curve at low frequencies.

acquired a tonal quality (Brecher). This tone was still extremely rough, and the roughness gradually declined as the frequency was raised further. This frequency therefore can properly be designated as the threshold of fusion (Brecher). It is practically the same for all the sensory modalities and is particularly well known in vision from the work in cinematography. In addition to 18 cps, a frequency of 9 cps is a good one for observing the discontinuity.

To study the discontinuous changes of loudness as a function of frequency a subject's threshold was measured in the following manner. In successive trials the sound pressure from the thermophone was reduced by steps of about 10 per cent, and the frequency was slowly raised automatically, starting from 2 cps, until an auditory sensation was aroused. The frequency thresholds corresponding to the various sound pressures are shown in Fig. 7-49. Below 4 cps and above 50 cps the discontinuity was not observed regularly or with certainty. For the measurements it

was convenient to provide the thermophone capsule with a small opening filled with compressed cotton, in order to keep the sound pressure constant or only slowly rising as the frequency was raised. (The thermophone current might have been changed continuously to produce the same result.) Unless the pressure was kept constant or nearly so, the stepwise character of the threshold could not be observed. It was further necessary to take care that no overtones were present, for the discontinuity was obscured by the presence of even slight noises and stray tones.

There was a high degree of constancy in the points of frequency at which the steps appeared. These points did not change as the sound pressure was raised to the threshold of touch or tickle. Also there was no

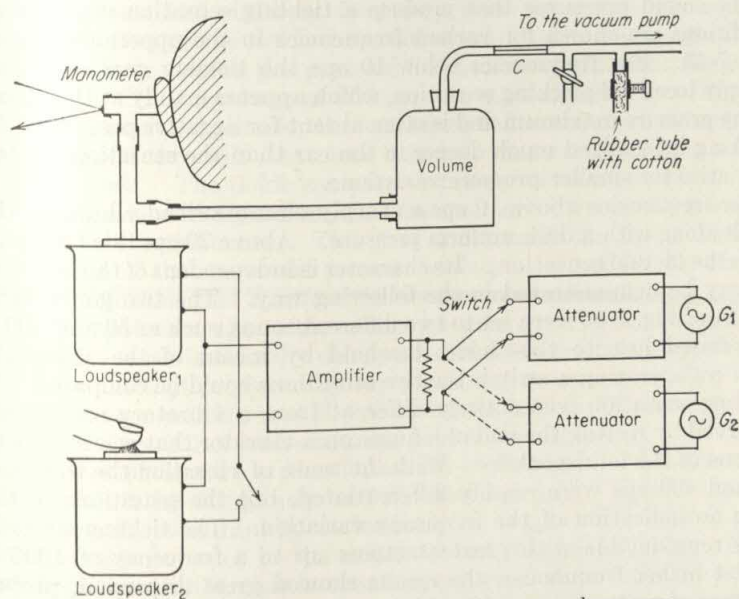


FIG. 7-50. Arrangement for the study of low-tone phenomena.

effect of a preliminary fatiguing of the ear with a powerful tone or the introduction of a static air pressure. There were slight variations, however, if the procedure was reversed and the frequency was varied from high to low instead of from low to high.

A fusion threshold in the region of 18 cps was found also with beating tones, as reported by Brecher. At the same time he observed a number of discontinuities in roughness.

Sensations of Tickle as Produced by Intense Tones. If the sound pressure applied to the external auditory meatus was increased gradually, a well-defined threshold was found beyond which any further stimulation produced a tickling sensation (see Helmholtz, 1; Fletcher, 1; Riesz, 1). The arrangement shown in Fig. 7-50 was used to study these phenomena.

In order to measure the sound pressure directly at the drum membrane, a T tube was used that was as short as possible relative to the wavelength

of the sound, and one end made an airtight connection to the external meatus. One arm of this tube was fitted with a calibrated membrane manometer, and the other arm transmitted the air-pressure variations of the electrodynamic loudspeakers L_1 and L_2 . For the lowest frequencies the loudspeaker was replaced by a pump and filter system as described earlier. A positive or negative static pressure could be applied to the ear also, and the manometer membrane served as well for the measurement of these values. This pressure could be varied by compressing the cotton-filled rubber tube. A capillary C and a volume were interposed so that a suddenly introduced static pressure would be applied to the ear gradually.

The sound pressures that produce a tickling sensation under normal conditions are shown for various frequencies in the uppermost curve of Fig. 7-48. For frequencies below 10 cps the tickling goes over into a sharply localized pricking sensation, which appears mainly at the moment of the pressure maximum and is often absent for negative pressure. This pricking is localized much deeper in the ear than the sensations of touch that arise for smaller pressure variations.

For frequencies above 10 cps a sharply circumscribed vibratory tickle is felt along with a dull, uniform pressure. Above 20 cps this tickle overrides the tactual sensation. Its character is independent of the frequency, as may be demonstrated in the following way. The two generators G_1 and G_2 of Fig. 7-50 were set to two different tones, such as 50 and 400 cps, and raised just to the tickle threshold by means of the attenuators. Now by operating a switch the two sensations could be compared. The tickling sensation was entirely different from a vibratory sensation, as observed by resting the end of a finger on a vibrator that was substituted for one of the loudspeakers. With the sense of vibration the frequencies 50 and 400 cps were readily differentiated, but the sensations of tickle gave no indication of the frequency variation. The tickling sensations were reproducible with great exactness up to a frequency of 1000 cps, but at higher frequencies the results showed great dispersion, probably because of resonances in the middle ear.

If the sound pressure was raised further, both the loudness and the intensity of the tickling continued to increase but in complete independence of one another. The tickling went over into an itching that extended to the auricle and often persisted for several minutes after the cessation of the tone.

In the region of the threshold the onset and decay times of the tickling sensation appeared when the beating complex reached its maximal amplitude, and this amplitude was the same as when a single continuous tone was used. If the beating rate was raised to 30 per sec, then the rhythmic character disappeared and the sensation became identical with that produced by a continuous tone.

To obtain precise measurements of the onset time for tickle, pulses of a 200-cps tone were used, with durations as shown in Table 7-5, and for each duration it was found how much the sound pressure p had to be increased in order to give the same tickle sensation as a tone of indefi-

nately long duration at a pressure p_0 . As may be seen in the table, the durations beyond 0.02 sec do not show any differences.

TABLE 7-5

Duration of pulse, sec.....	0.005	0.010	0.015	0.02	0.04
p/p_0	3.0	1.7	1.1	1.0	1.0

The following procedure was used to ascertain whether the tickling sensation arises at the same location for all frequencies, or whether this sensation exhibits a spatial localization as in hearing. Two stimuli of equal pressure and different frequency were superimposed, and their combined effect on the tickle threshold was studied. The results showed that to a large degree the pressure amplitudes of different frequencies are added. Thus if a tone of 200 cps was superimposed upon one of 50 cps of the same amplitude, the combined tones required an amplitude for the tickle threshold that was only half that required for one of the tones by itself. The tickle sensation is mainly determined by the maximal amplitude of the pressure, and the manner in which the pressure is attained has no influence. This it is understandable that a distortion in the form of the sinusoidal pressure variation can affect the threshold only to the extent that it alters the maximum amplitude.

If observations of the tickle sensations were continued for a month or more, these sensations finally disappeared and were replaced by a burning sensation like that produced by rapid rubbing on an area of skin. This effect was very painful, and the observations had to be discontinued to prevent the arousal of long-enduring pain in the middle ear.

Loudness of Sounds at the Threshold of Tickle. It is known, from measurements by Kingsbury and by Fletcher and Munson, that low tones increase more rapidly in loudness for a given increase of sound pressure than do tones in the middle of the frequency range. Hence, in spite of a great difference in threshold pressure, these tones have nearly the same loudness at a pressure of 10 dynes per sq cm. For tones below 20 cps a comparison of loudness with the reference tone of 1000 cps is extremely difficult, and the great difference in the character of these tones produces a wide dispersion in the observations. Therefore these low tones were compared with a tone of 50 cps, whose loudness relations to the reference tone had already been determined.

In Fig. 7-51 the abscissa shows the sound pressure for tones of 5 and 10 cps relative to the pressure at their thresholds, and the ordinate shows in the same way the relative sound pressures required for an equally loud tone of 50 cps. It is clear that the slope of the loudness curve is increased for tones below 50 cps. The results might be taken to signify that at the point at which the auditory threshold curve crosses the threshold curves for tickle and pricking, as represented in Fig. 7-48, a relatively small variation of pressure ought to encompass the whole range of loudness changes, a range that for 1000 cps requires a variation of ten-millionfold. But because the tickle sensations arise in the middle

ear and are entirely independent of the loudness sensations, the tickle curve ought not to be regarded as an equal-loudness function.

To test this point more specifically, the sound pressure was adjusted to the tickle threshold for various frequencies, and the loudness of these tones was then compared with that of a tone of 1000 cps. The results are given in Fig. 7-52 with the level expressed in decibels above threshold of a 1000-cps tone of equal loudness. It is evident that there is a regular decrease of loudness as the frequency is lowered. In this procedure the loudnesses of the oscillating pressures below 20 cps were again measured indirectly, in that a comparison was first made of their loudnesses with that of a tone of 50 cps.

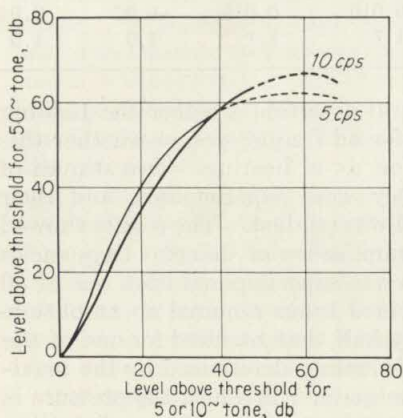


FIG. 7-51. The loudness of tones of 5 and 10 cps expressed in terms of a tone of 50 cps.

upon the tickle threshold. For tones below 100 cps, however, the loudness is rising only slowly even before the tickle threshold has been reached. Beyond the tickle threshold only a slight increment of loudness can be obtained. For pressure oscillations below 20 cps the loudness

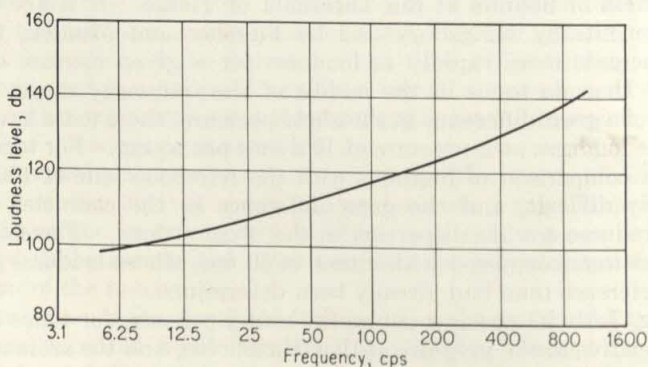


FIG. 7-52. The loudness of various tones at the tickle threshold.

has even begun to fall beyond the tickle threshold, as shown by the dotted curve in Fig. 7-51.

It is possible that this phenomenon is related to the maximum discharge of the auditory nerve, as observed by Davis (1) and his associates. Unfortunately, the measurements of auditory-nerve impulses have been limited to one region of frequency, and it cannot be concluded with

certainty that for the low tones the maximal frequency of the nerve currents will be smaller than it is for the high frequencies. At 1000 cps the maximal loudness is about 50 db greater than can be obtained at 10 cps.

It may be considered also, as shown in Fig. 7-48, that at the low frequencies the effective value of the sound pressure has attained values beyond 10,000 dynes per sq cm, and therefore it may be calculated from the impedance of the eardrum that the amplitude of vibration of the eardrum will be of the order of 0.2 to 0.4 mm. This amplitude can no longer be considered small relative to the dimensions of the ossicles. Thus it seems possible that the ossicles are deflected away from their normal positions of vibration, and accordingly the transmission of vibrations to the inner ear is impaired. This would mean that the middle

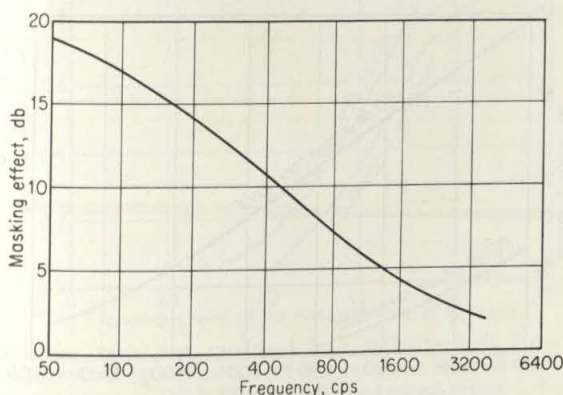


Fig. 7-53. Masking of a 10-cps tone produced by tones of various frequencies and a loudness level of 80 db.

ear provides a mechanism for protecting the inner ear against frequencies below 50 cps, which are of common occurrence in particularly powerful magnitudes (F. Trendelenburg, 2). In favor of this suggestion is the fact that when a static air pressure of 10 cm of water is superimposed upon an oscillatory pressure of 10 cps the rise of loudness is even smaller than usual.

Raising of the Auditory Threshold as a Result of Masking. The investigations of masking begun by Wegel and Lane were extended to the low tones. A study was made of the elevation of the threshold of a 10-cps tone when the ear was simultaneously exposed to masking tones of a loudness level of 80 db. In Fig. 7-53 the abscissa shows the frequencies of the masking tones, and the ordinate shows how much the pressure of the 10-cps tone had to be increased to make it audible once more. It is evident from the figure that the masking effect is relatively small. This is in agreement with auditory theory. If the loudness of the masking tone was less than 50 db above threshold it was no longer possible to observe with certainty any effect upon the 10-cps tone.

The masking of tones of high frequency by a 10-cps tone is represented in Fig. 7-54. Here the ordinate shows how much the threshold is raised for the various tones indicated on the abscissa. The amplitude of the 10-cps stimulus was either 20 or 40 db above its threshold (sound pressure 200 or 2000 dynes per sq cm). Here also it appears that masking operates over a wide range of frequency. This masking does not arise in the middle ear, but in neural processes. This fact was proved by exposing the ear for 2 or 3 min to the 10-cps tone and then immediately determining thresholds for the various frequencies. The results showed a raising of the threshold that varied with frequency in the same manner as observed for masking.

Because a static positive or negative air pressure produces a change in the impedance of the eardrum, it is to be expected that the loudness of a

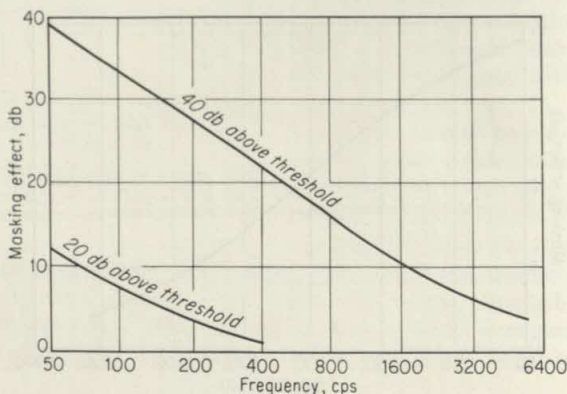


FIG. 7-54. Masking of various tones by 10 cps when presented at 20 and 40 db above threshold.

tone will undergo regular alterations when slow oscillations of air pressure are presented simultaneously. For a 10-cps tone this phenomenon is readily observed. In order to measure the effects, the left ear was stimulated with a constant tone of 1000 cps together with a tone of 1010 cps whose amplitude was adjusted to give to the ten beats per second the same loudness variations as observed in the right ear for a tone of equal loudness with a superimposed 10-cps tone. Figure 7-55 shows the intensity of the modulations of loudness in a tone of 1000 cps and at two different loudnesses, with the intensity modulations measured by the ratio of maximum to minimum amplitudes of the beating tone.

When the sound pressure of the 10-cps tone was less than 20 db above threshold there was no modulation at all. The eardrum and the middle ear then continued to operate in a completely linear fashion. But if the sound pressure became greater (*i.e.*, over 2000 dynes per sq cm), the weak tones especially were modulated (*cf.* page 339). As the figure shows, the 10-cps tone when 30 db above threshold produced nearly a complete modulation of a 1000-cps tone that had a loudness level of 30 db.

The phenomenon is independent of the frequency of the tone being modulated, for tones of equal loudness over a range from 100 to 4000 cps gave about the same degree of modulation.

If these observations were carried out with the arrangement shown in Fig. 7-50, by replacing the static pressure apparatus with the generator of low tones, then it might happen that the diaphragm of the dynamic loudspeaker was displaced from its normal position by the action of the air-pressure variations. This might give a modulation of the 1000-cps tone by an action in the loudspeaker itself. To check this possibility the sound was listened to from the other side of the loudspeaker diaphragm (the side that was not exposed to the 10-cps pressure variations). The

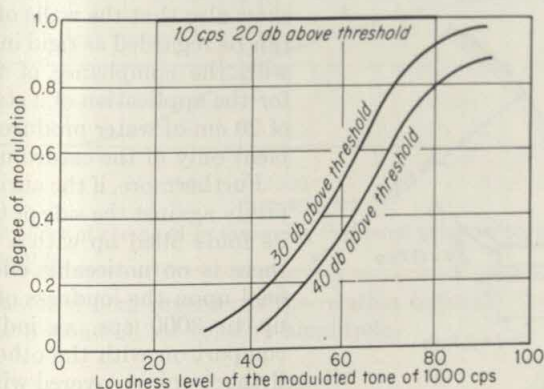


FIG. 7-55. Loudness variations produced in a 1000-cps tone by a superimposed 10-cps tone, represented as a function of the loudness level of the 1000-cps tone. The minimal sound pressure divided by the maximal sound pressure during the modulation represents the degree of modulation.

sound emitted from this side of the diaphragm was completely smooth, and therefore the modulation was not produced by the loudspeaker.

EFFECTS OF THE HEAD AND EXTERNAL AUDITORY MEATUS ON THE SOUND FIELD*

Most explanations of the variations in auditory thresholds obtained by different methods make reference to the difference between the sound pressure in a free field and that acting upon the eardrum (*cf.* Hahnemann and Hecht; Waetzmänn, 4; Langenbeck, 1; Waetzmänn and Heisig). This difference arises from reflections of sound by the head, resonances in the external auditory meatus, and variations in the compliance of the eardrum. Some of these effects can easily be calculated, for they are similar to the ones concerned in the calibration of a microphone as worked out by Ballantine (2; see also West, 3).

If a plane wave impinges upon a flat water surface, the ratio between the vibratory amplitude of the reflected wave and that of the incident

* Article 12 as listed in the Author's Bibliography. Published in 1932.

wave is a minimum when the incident wave is perpendicular to the surface. If ρ_1 and ρ_2 are the densities and c_1 and c_2 are the velocities of sound for air and water respectively, then a minimum is obtained as

$$\frac{\rho_2 c_2 - \rho_1 c_1}{\rho_2 c_2 + \rho_1 c_1} = 0.9994$$

This condition represents a practically complete reflection of the sound wave. The acoustic stiffness of bone covered with skin is equal to or exceeds that of water, and therefore no serious error will result if the head and meatus, apart from the eardrum, are regarded as completely rigid in respect to aerial vibrations. Observations with an ear microscope

show also that the walls of the meatus can be regarded as rigid in comparison with the compliance of the eardrum, for the application of a static pressure of 20 cm of water produces a displacement only of the eardrum.

Furthermore, if the auricle is pressed firmly against the side of the head and its folds filled up with a plastic mass there is no noticeable effect in a free field upon the loudness of frequencies up to 3000 cps, as indicated by a comparison with the other ear. Also if the trunk is covered with absorbing material so as to reduce its reflections of sound, we can replace the head approximately by a rigid sphere of similar size. In the sphere, as Fig. 7-56 shows, a round hole represents the meatus. Its length and width

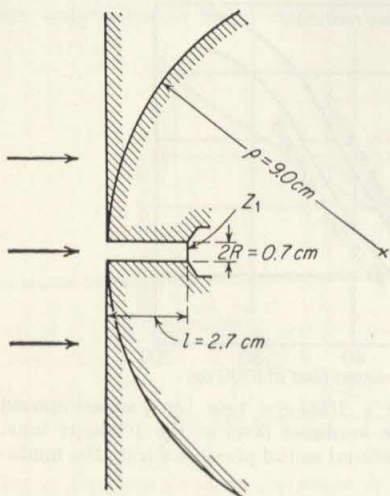


FIG. 7-56. Simplified dimensions of the external auditory meatus and the head.

were determined by filling a large number of meatuses with Wood's metal. The end of the hole is closed by the eardrum.

If plane waves of sinusoidal form are directed toward the meatus and their sound pressure in the free field is p , then according to Ballantine's calculations on a basis of Thévenin's theorem and the analogical relation between acoustical and electrical systems, the vibratory amplitude of the air particles at the entrance to the meatus is given by

$$\dot{x}_0 = \frac{p_0 S}{Z_k + Z_0} \quad (7-5)$$

Here $S = \pi R^2$ represents the cross section of the meatus, and p_0 is the sound pressure at the entrance of the meatus when it is fitted into the surface of the sphere.

The ratio between this sound pressure p_0 and the pressure of the free field p was also calculated by Ballantine, and is represented as a function

of frequency for the present situation in Fig. 7-57. The points shown in this figure represent measurements made by Langenbeck (1) by means of a small microphone placed directly on the skin of the head. Because the sound source was located 30 cm from the head there were reflections between the source and the head, and consequently a dispersion of the measurements apart from the variations arising from the spherical form of the sound field.

In the above formula Z_K represents the acoustic impedance of a vibrating piston in the meatal opening as viewed from inside the meatus.

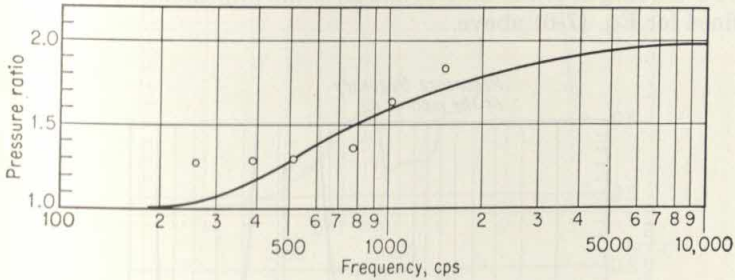


FIG. 7-57. The effect of the head in increasing the sound pressure at the entrance of the external meatus.

Impedance as used here represents the relation between the total force acting on the piston and its velocity amplitude,

$$Z_K = \frac{p_K S}{\dot{x}_0} \quad (7-6)$$

This value cannot be calculated for the piston vibrating at the surface of the sphere. Therefore the surface of the sphere has to be replaced by a plane surface, as shown in Fig. 7-56. Experimental tests made in connection with the calibration of microphones show that only a slight error is introduced by this procedure. In the present situation the error is even smaller because Z_K is small relative to Z_0 (the impedance of the meatus) in the frequency region concerned.

If R is the radius of the meatal opening, ω is the angular frequency of the sound pressure, and $k = \omega/c_1$, then according to Rayleigh's calculations (see Crandall)

$$Z_K = \rho c S \left[1 - \frac{J_1(2kR)}{kR} + i \frac{K_1(2kR)}{2(kR)^2} \right]$$

Here the terms enclosed in square brackets can be transformed as follows:

$$1 - \frac{J_1(2kR)}{kR} = \frac{k^2 R^2}{2} - \frac{k^4 R^4}{2^2 \times 3} + \frac{k^6 R^6}{2^2 \times 3^2 \times 4} - \dots$$

$$\frac{K_1(2kR)}{2(kR)^2} = \frac{4}{\pi} \left[\frac{2kR}{3} - \frac{(2kR)^3}{3^2 \times 5} + \frac{(2kR)^5}{3^2 \times 5^2 \times 7} - \dots \right]$$

Because in this situation kR is extremely small, it is sufficient to consider only the first term of the series. In fact, for frequencies below 3000 cps, $kR < 0.192$, so that even the first term will give values within 1 per cent of the correct ones. Z_0 represents the impedance of the meatus, and according to transmission-line theory

$$Z_0 = \rho c S \frac{Z_l \cos kl + i \rho c S \sin kl}{\rho c S \cos kl + i Z_l \sin kl}$$

where l is the length of the meatus and Z_l is the impedance of the eardrum as defined for Eq. (7-6) above.

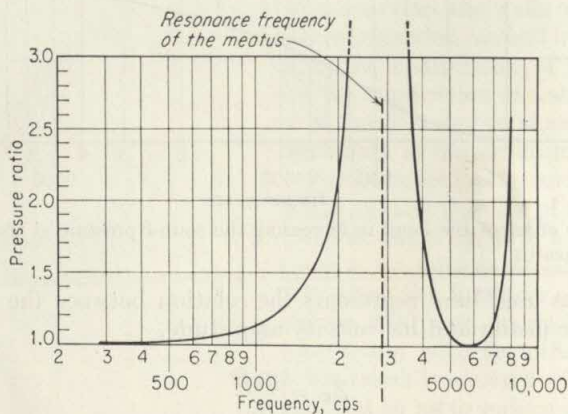


FIG. 7-58. Increase of pressure at the eardrum due to resonance of the meatus when the eardrum is rigid. The broken line indicates the resonance frequency of the meatus.

From the amplitude of vibration $\dot{x}_0$ of the air particles at the entrance of the meatus as obtained from Eq. (7-5), the actual pressure on the eardrum according to transmission-line theory is

$$p_l = \rho c \dot{x}_0 \frac{Z_l}{\rho c S \cos kl + i Z_l \sin kl} \quad (7-7)$$

From this may be obtained the ratio between the pressure at the eardrum p_l and the pressure p of the free field.

If the eardrum were completely rigid, then $Z_l = \infty$. For this condition there will be an increase in sound pressure p_l/p_0 as a result of resonance in the meatus, as Fig. 7-58 shows.

To obtain the increase of pressure for the normal ear, we may take for Z_l the value of eardrum impedance obtained by Tröger. These values have to be multiplied by S in order to satisfy the conditions of Eq. (7-6). Because at frequencies above 800 cps the eardrum in its vibration breaks up into parts, there are several points of resonance in this increase of pressure, as Fig. 7-59 indicates.

Figure 7-60 shows the total increase of pressure produced by the head and the meatus in the normal ear. These values were obtained by multiplying those of Fig. 7-59 with those of Fig. 7-57.

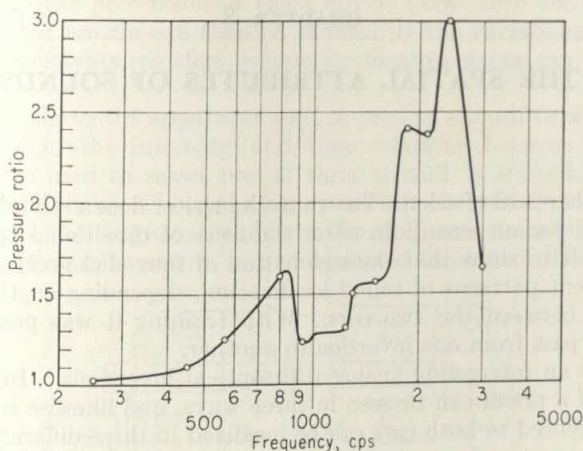


FIG. 7-59. Pressure increase due to resonance of the meatus when the eardrum is normal.

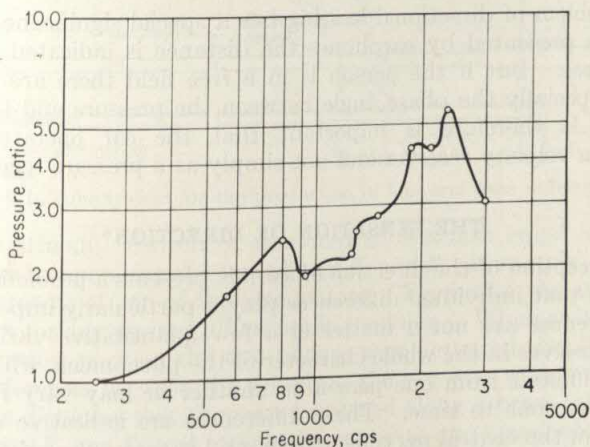


FIG. 7-60. Combined effect of head and meatus.

If the velocity amplitude $\dot{x}_0$ is not produced by an external sound field but by a piston vibrating in the opening of the meatus, then Eq. (7-7) may be used to calculate the sound pressure acting on the eardrum, with the compliance of the eardrum taken into the account (see above, page 136).

CHAPTER 8

THE SPATIAL ATTRIBUTES OF SOUNDS

In no other field of science known to the writer does a stimulus produce so many different sensations as in the area of directional hearing. It was possible to show that the summation of four clicks can give rise to four different patterns of sound localization, depending on the types of inhibition between the two ears. With training it was possible for a subject to pass from one inversion to another.

There is an interesting analog with optical inversions. In vision the drawing of a prism can be seen in three ways, and likewise in hearing a sound presented to both ears can be localized in three different places.

A further reason for a special interest in directional hearing is that this sort of sensation can be pointed to and therefore can be measured in numerical terms.

The problem of directional hearing has a special significance also. If a sound is presented by earphones the distance is indicated simply by the loudness. But if the person is in a free field there are additional factors, especially the phase angle between the pressure and the particle velocity. It therefore is important that the ear operate in some degree as a velocity receiver and not simply as a pressure receiver.

THE SENSATION OF DIRECTION*

The perception of the direction of sounds presents a problem of special interest in that individual differences play a particularly important role. The differences are not a matter of a few quantitative variations but show themselves in the whole character of the phenomena, which may be entirely different from one person to another or may vary for a given person from time to time. These differences are indicative of complex processes in the central nervous system, and it seems clear that the complex stimuli affecting the two ears are combined in some higher center to produce a unitary sensation. Even though the actual excitations may vary only in limited ways, it is possible for their combining to take a great variety of forms. The resulting perceptions then may depend on rather subtle variations of timbre and loudness that ordinarily go unnoticed, so that the variations in the phenomena may seem chaotic and incomprehensible. Yet after a subject has been presented with all possible forms of stimulation, he gradually learns to recognize all the

* Article 5 as listed in the Author's Bibliography. Published in 1930.

types of phenomena, and after sufficient practice can voluntarily switch from one to another. It is then possible to arrange the various observations into the proper stimulus categories, so that most of the individual differences in the perception of them can be taken into account. The differences that remain can then be handled by the variations of a small number of constants, so that systematic measurements can be carried out.

Figure 8-1 shows the apparatus used to present stimuli to the two ears with control of the intensity and time relations between them. A switch S was used to select one of three stimuli: a sinusoidal tone, a noise, or a brief click. Clicks of a highly uniform character were produced by charging or discharging a condenser C with direct current through the resistance. Two attenuators b_1 and b_2 served to control the intensities

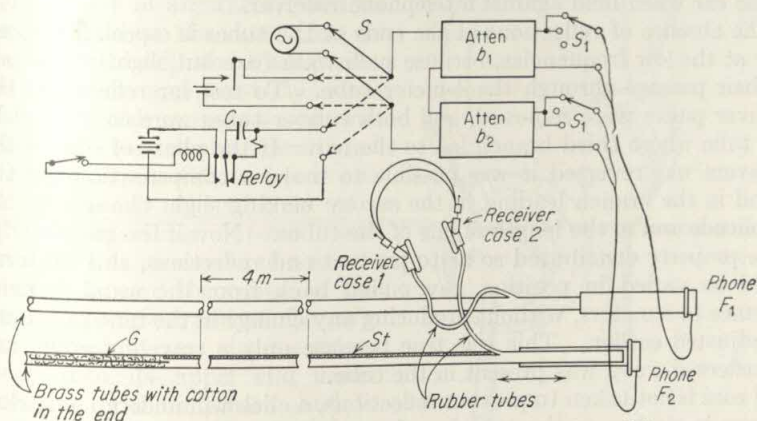


FIG. 8-1. Tube system for the production of binaural time differences.

of the two stimuli. Switch S_1 was used to establish equal loudness in the two ears by operating the two phones F_1 and F_2 alternately, with suitable adjustments of one of the attenuators. Thereafter the attenuators could be set for any desired difference in loudness. When switch S_1 was in its uppermost position the two phones were actuated simultaneously.

Time differences between the sounds at the two ears were produced by varying the distances that the sound traveled along a brass tube. Each of the phones F_1 and F_2 was attached securely to one brass tube to which another brass tube was fitted so as to slide smoothly. A rubber tube ran off from the longer tube at a point about 1.5 meters from the end, and was attached to the case of a telephone receiver to provide a comfortable way of listening. The length of the sound path could be varied by sliding the outside tube that was attached to the phone. The tubes had to have a large diameter to prevent a change of sound intensity as the path was varied. Usually this diameter was 3 cm. The arrangement permitted a change of path length of 40 cm with less than a 5 per cent change in sound pressure, and for the highest frequencies used this did not affect the perceived direction.

With tubes of this diameter there is little damping of the sound waves, and to avoid resonance it is necessary to prevent reflections. Therefore the tube system was kept straight and of uniform diameter. The wall thickness of the longer tube was less than 0.2 mm at the place where it joined the phone. A rod of the same diameter as the inside diameter of the rubber tube was placed within the brass tube beyond the junction with the rubber tube so as to give a uniform cross section. The far end of the brass tube was loosely filled with pieces of gauze tied to a thread to provide damping of the sound waves and prevent any reflection from this end.

The inside diameter of the rubber tubes leading to the ears was 6 to 7 mm, and was so chosen in order to prevent reflections at the ears. West (2) has shown that tubes of this size have about the same impedance as the ear when held against a telephone receiver.

The absence of reflections at the ends of the tubes is especially necessary at the low frequencies, because such waves are but slightly damped in their passage through the 4-meter tube. To test for reflections the receiver pieces were removed, and both rubber tubes were connected to a T tube whose third branch led to the ear. If the phase of one of the receivers was reversed it was possible to make a compensation for the sound in the branch leading to the ear by making slight changes in the amplitude and in the length of one of the tubes. Now if the gauze strips were properly distributed so as to prevent end reflections, this material could be varied in position, say pulled back from the usual 4-meter distance to 5 meters, without producing any change in the tone minimum as adjusted earlier. This was true because only a traveling wave and no reflected wave was present in the tube.

If care is not taken to prevent reflections, a click will undergo a marked change in timbre as the tube length is altered. The result is a serious disturbance of the observations.

The slight difference in wave velocity in the tube compared with that in free air was of no importance, because all the measurements were concerned with relative time differences.

If now equality of loudness was established in the two ears and then one tube was varied in length, the subject ordinarily perceived a sound image that was well defined, about 2 cm broad, and seemed to be floating in space a short distance outside the head. This experience was especially easy to obtain with clicks. As the time difference was increased between the two sounds the image moved still farther to one side, until for a certain time difference $\Delta t = k$ it came to lie nearly on the line of the two ears. From there on, the velocity of its movement decreased greatly. The constant k is called the Hornbostel-Wertheimer constant.

In the course of the measurements it was often important to fix the location of the image in space. Then the fluctuations of the image arising from temporal changes in the nervous system, from fatigue, and the like, could be evaluated. This was done by placing about the head a semi-circular scale on which the direction of the image could be read off. This procedure became fatiguing in the course of time, apart from the fact

that the estimates of direction were inexact, for the subject did not know from what central point the image was to be projected upon the scale. A better procedure will now be described.

If the intensity of the click is increased, the circle on which the sound image moves becomes smaller until at a certain value it seems to be moving directly on the skin of the forehead. A click can give exactly the same sensation as if a blunt object were tapped against the forehead. The exact place can be perceived, and hence the direction is well indicated. For long-continued observations a small, momentary jet of air was applied to the forehead at the same time as the click and adjusted by the subject so as to appear at the same spot. For this purpose a scale was fastened to the telephone headband as shown in Fig. 8-2, and to it was fastened an air tube with its main portion extending outward and downward as pictured and a nozzle pointing toward the center of the scale. The lower end of the tube was held shut, and air was introduced into its upper end under pressure. The air stream had to be pulsating, because a steady one soon became imperceptible as a result of adaptation. This arrangement permitted a determination of changes of direction up to 80° as measured from the center point.

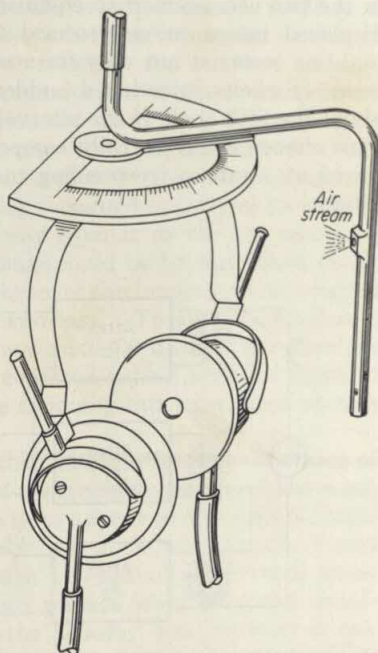


FIG. 8-2. Arrangement for determination of the direction of a sound.

The usefulness of the apparatus is indicated by the fact that when the conditions were arranged so that one sound image coincided exactly with another produced by a second pair of tubes, the dispersion of the tube settings was of the same magnitude as the adjustments of the air tube to the image. The simplicity of this observation depends upon the fact that tactual space and auditory space have much in common. Indeed, the whole character of the sensation has its anatomical basis in the fact that the labyrinth is an outgrowth of the skin which at a late stage is cut off and then continues to develop separately.

Effects of Fatigue. If the auditory nerves are exposed to prolonged stimulation their characteristics are somewhat changed. This change is called fatigue.* An alteration in the direction of a sound can arise when the nerve endings of the basilar membrane are exposed to progres-

* This term is used here for what some have called fatigue, others have called adaptation, and some have regarded as a combination of the two.

sive fatigue by a sound of constant intensity, because the excitatory effect in the nervous system becomes smaller with the passage of time. This form of change in direction was particularly noticeable when the sound intensity was different in the two ears. Then, when the sound was intense, the fatigue appeared rapidly (see page 357), and the intensity in the two ears seemed to equalize, while at the same time the laterally displaced image moved toward the mid-line. This shift toward the mid-line occurred not only for a continuous tone, but equally well for a series of clicks introduced suddenly. A noticeable shift appeared at about the fifth click, if the interval between successive clicks was 1.0 sec. This change could be fully compensated for if the sound intensity was raised at a rate corresponding to the loudness decrease caused by the fatigue.

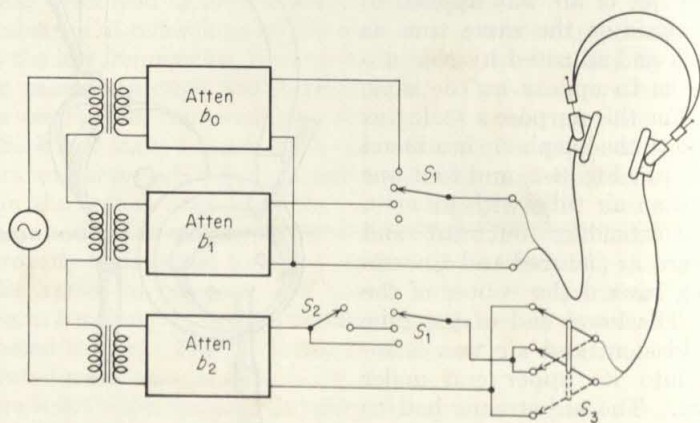


FIG. 8-3. Circuit for determining the effect of fatigue on the direction of a sound.

It is also conceivable that the effect of fatigue on the time difference between the two ears is due to changes in the latency of firing of the nerve endings or the rate of conduction of the excitatory pulses. It was found, however, that if care was taken to keep the loudness relation in the two ears constant, there was no effect of fatigue on the direction of the sound. This was true both for continuous tones, for which latency hardly comes into play, and for clicks, for which both latency and conduction rate may operate. Therefore we can attribute the effects of fatigue on the direction exclusively to the changes of loudness. That there are no alterations in rate of conduction is attested by the well-known fact that the central nervous system is much less subject to fatigue than the nerve endings.

The circuit shown in Fig. 8-3 was used for observations on continuous tones. When switch S_2 was open, the attenuators b_1 and b_2 were adjusted so that when switch S_1 was shifted between positions 3 and 4 the loudness was equal in the two phones. When S_2 was switched to its lowermost position and S_1 to the next-to-the-lowest position, the two phones were actuated simultaneously; and when their polarity was correct as deter-

mined by S_3 , the sound image was maintained for the most part in the mid-line. Then S_1 was set in the upper position, and one ear was fatigued for 2 min with a tone of an intensity set by b_0 at 10 dynes per sq cm. Preliminary tests showed how much b_1 had to be changed to compensate for the fatigue and keep the loudness equal in the two ears by switching S_2 and S_1 successively to the four positions. A delay of 1 sec was made at the second position, where no tone was produced, because immediately after the ear was fatigued the loudness changed relatively rapidly and no precise and reproducible loudness comparisons could be made. At the two lower steps the delay was 0.5 sec. After these preliminaries it was found that after the fatigue, with S_1 at the next-to-the-lowest position, with S_2 on, and with a delay of 1 sec, the sound image at the moment of switching remained exactly in its original location and then gradually shifted away from it as the ear recovered from its fatigue. By shifting b_1 the image could be brought back to the mid-line and the fact confirmed that whenever the image took its original position the loudness was equal in the two ears. To obtain a maximum amount of fatigue, the fatiguing tone was made 20 db stronger than the tone being observed. If the test was repeated with a series of clicks, it was best to use the same clicks for the fatiguing but with much shorter intervals between them.

It was found by Bartlett and Mark that long-continued observation of a sound image affects the direction of a successive image of the same kind. Thus if a tone was presented so as to appear at the extreme right for a long time and then the stimulation was such as ordinarily would give an image in the mid-line, the image was actually perceived as on the left. To study this effect, the two phones were actuated simultaneously and at equal loudness, and the polarity was reversed in one phone. The image then appeared far to one side for frequencies between 300 and 800 cps. Lower frequencies did not give this effect, because for them a reversal of phase produced so large a temporal disparity that the image split in two, one portion appearing in each ear. If after a certain time switch S_3 was again reversed so that the phones had the correct polarity once more, the image appeared at exactly the same place as usual. Thus an aftereffect of one image on another could not be observed. The same result was obtained also by varying the time differences by means of the tube system.

If tubes of small diameter were used, however, this effect could be obtained. When both time and loudness relations were equal in the two ears, the image was in the mid-line. Then if the tube to the right phone was made longer, the image shifted to the left. If this direction of the image was observed for a long time, the right ear became fatigued to a somewhat greater extent than the left ear, because the sound was stronger in the shorter tube. If at this point the tubes were again made equal in length, the tone on the right seemed the louder, and the image shifted to the right.

When the fatigue was the same in the two ears the direction of the sound image was unaltered, and this was true irrespective of the direction

of the sound image to begin with: the same happened for an image lateralized to one side as for one in the mid-line (*cf.* Pattie). Another way of saying this is that the Hornbostel-Wertheimer constant k is unaffected by fatigue.

Paths Followed by the Sound Image. Figure 8-4 shows how the sound images shift as a result of temporal disparities. As the temporal disparity increases, the image shifts backward from the mid-line along an arc until for a certain disparity $\Delta t = k$ the direction of movement changes abruptly and the image moves sharply away from the head.

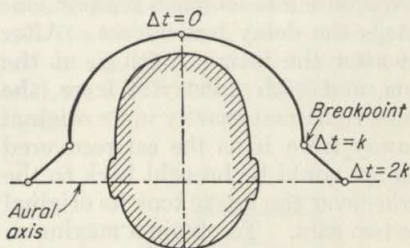


FIG. 8-4. Path of the sound image.

Thereafter the backward movement is only slight. When a disparity of $\Delta t = 2k$ is reached, this backward movement ceases, and for still greater disparities the image remains motionless until at last the image breaks up into two. The entire movement of the image thus takes place in a temporal span of $2k$, of which the first half leads to the sharp break in the path. These relations are shown in Table 8-1 for four subjects, for which different sound intensities were used at the beginning to locate the image in the mid-line. The table shows the extent to which the tubes had to be shifted to displace the image from the mid-line to the break point, and from the break point to the extreme lateral position.

TABLE 8-1

Sub- jects	A, shifting from mid-line to break point	B, shifting from break point to one side	Ratio of B/A
1	8.25	10.9	1.32
2	7.2	7.6	1.05
3	21.6	19.0	0.88
4	14.2	13.7	0.97
			Mean value 1.06

Many persons had difficulty in perceiving any movement at the point where the temporal disparity was reduced just below $\Delta t = 2k$, and went on to $\Delta t = 1.5k$ where the image first changed from the extreme lateral position. This was often the case when the intensity was great, for then the sound image seemed large and ill-defined, so that a small movement was difficult to judge. Others, however, gave repeated settings of the tubes that were correct to the centimeter, and for them the two tubes always gave the same settings.

The entire path of movement of the sound image lies in a single plane, which is horizontal when the loudness is small but becomes inclined forward when the intensity is raised, until it comes to lie in a vertical

semicircle for the strongest sounds. Moreover, as the loudness increases the two break points move farther away from the axis of the ears, so that they show a smaller lateral displacement. At the same time the whole pattern of the sound path is diminished until finally it lies entirely within the head.

To observe these phenomena it was found best to use a continuous series of clicks, because their direction is most clearly perceived. As indicated in Fig. 8-5, the click was produced by means of a rotating switch, with a rate of one interruption per second, used to charge and discharge a condenser into the attenuators and phones. Switch S_0 was used in adjusting for equality of loudness in the two ears, and switch S_1 was used to vary the loudness of the sound image. When the sound image had been shifted to one side by introducing a time disparity, such an

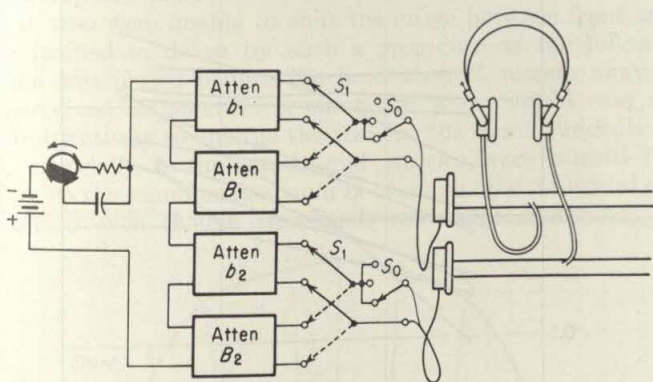


FIG. 8-5. Arrangement for determining the effect of sound intensity on sound direction.

increase in loudness led to a reduction in the distance from the mid-line in most subjects. This effect depends upon the fact that, as loudness increases, k becomes larger; and so, according to the Hornbostel formula, $\Delta t = k \sin \phi$ (ϕ represents the angular displacement from the mid-line), the time disparity produces a smaller lateral displacement. This change in k could be evaluated if with the louder stimuli the time difference Δt was enlarged until the displacement became equal to that with the weaker stimuli. Then the two values of k behaved like the corresponding time differences.

More precise values were obtained if one tube was left in position and the other was shifted by the amount necessary to pass from the break point on one side of the image pattern to the break point on the other side. Figure 8-6 shows for a number of subjects the corresponding time difference $2k$ as dependent upon sound intensity. As is evident, the relationship is highly variable; yet in general the value of k varies nearly in proportion to the loudness level of the sound (measured in decibels above threshold). The values of k also change considerably from time to time.

With a few subjects at times the value of k did not change at all with sound intensity. With them also k was unaffected by previous stimulation. Such subjects gave the most uniform results in a series of measurements.

The degree of dependence of k upon sound intensity provided a good way of choosing the most satisfactory subjects for a series of measurements. Such subjects after only a little practice gave results that otherwise would have had to be obtained as averages of a great many measurements. Apparently this condition, in which there is only a limited effect of stimulus intensity on nerve activity, is a general characteristic of the nervous system of these subjects.

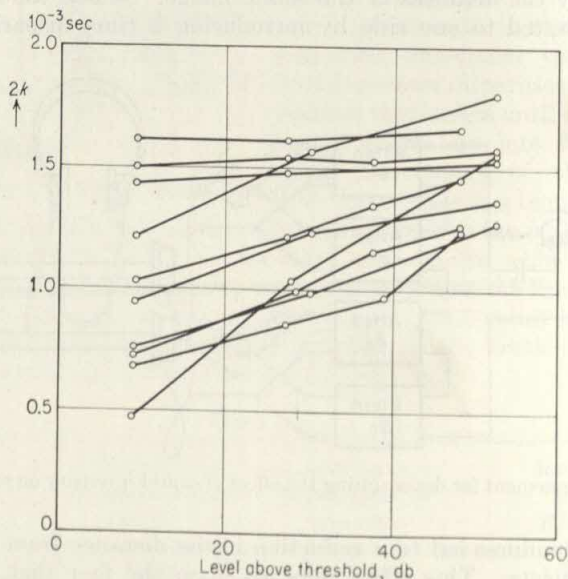


Fig. 8-6. The effect of sound intensity on the Hornbostel-Wertheimer constant.

We return to a consideration of the path of movement of the sound image. When a sound source is moved about, a subject whose eyes are closed can report with complete accuracy where the source is, how far away, and whether it is in front or behind. But under the conditions of these experiments a number of the cues were lacking that normally determine distance, position, and the like. In the experiments only the sound intensities and their contrary relations in the two ears together with the time relations were considered as variable attributes of the presentation. Perception of the distance of a sound depends upon characteristics of the sound field that still are not well understood, but in the experimental situation the apparent distance was determined simply by the loudness. The less the loudness, the farther away from the head the sound image seemed to be, and when the loudness remained constant this distance was always the same. However, the conditions

were indeterminate as to front-back location. It was possible for a subject voluntarily to shift the image from front to back or vice versa. These conditions have an analogy in vision in the perception of reversible perspective figures, like the one shown in Fig. 8-7, where the shaded surface can be seen as in front of, or behind, or on the same plane with the other surfaces.

Figure 8-8 shows results obtained in a subject who ordinarily perceived the sound image in front of the head, but who was able to shift it to the back. It is seen that the posterior path is considerably flatter and closer to the head than the anterior path, though the lateral displacements are the same.

Subjects who were unable to shift the image between front and back could be trained to do so by such a procedure as the following. A metronome was placed behind the head about 5 meters away; it was clearly perceived as behind. If the hands were cupped over the two ears, so as effectively to enlarge the auricles, the sound suddenly jumped forward, especially if the hands and auricles were pushed forward. With practice the sound image could be made to take a forward or backward position even though the hands were kept motionless. Many

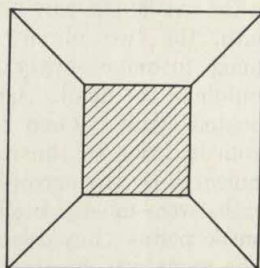


FIG. 8-7. A drawing showing reversible perspective.

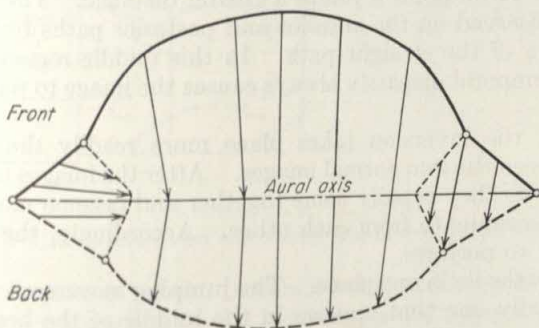


FIG. 8-8. Anterior and posterior paths of the sound image.

subjects were able to make the image jump back and forth without this use of the hands. The distance of the image from the head did not need to change. What this means is that many conditions are operating simultaneously, and voluntarily certain ones can be emphasized or minimized. In this process the slight distortions of sound produced by the auricle are neglected, though ordinarily these provide a basis for our discrimination of front and back.

The analogy between optic and acoustic inversion can be carried further. Optically there are three possibilities, one of them having one dimension less, as can be seen in Fig. 8-7, where the drawing can be regarded as a flat frame as well as two tridimensional figures. Also in hearing there are three possible sound paths. The first two, which

have already been described, form plane curves; the third path is a straight line, as shown in Fig. 8-8 by the dot-dash line running parallel to the axis of the ears and about 1 cm away from it. To locate this third path, the two phones were sounded alternately, causing the sound image to move slowly from either extreme lateral position toward the middle of the head. Once this path had been experienced it was readily located again. Then the subject could readily make the image jump from in front to the middle path, or from here to the one in back, as indicated by the arrows in Fig. 8-8. These lines of passage between the paths were mostly inclined at small angles as indicated, until near the break points they reached a maximum of about 15° on the average. The angle was greater if the jump was made first to the middle path, because the image moved more toward the middle of the head; and then on going farther the image moved away again. All subjects but one noticed this effect.

Besides these three pathways, one more was found, though it was limited to the region between $\Delta t = k$ and $\Delta t = 2k$. If the time difference was enlarged beginning with the break point the image often moved to the inside of the head instead of outward. This peculiarity has frequently been mentioned in the literature on sound localization. Both paths can be inverted, so that the image jumps back and forth in a direction nearly parallel to the axis of the ears. As the image gets farther away from the break point it jumps a greater distance. These inversions can also be observed on the anterior and posterior paths but not on the middle portion of the straight path. In this middle region an enlargement of the temporal disparity always causes the image to pass out of the head.

In general, the inversion takes place more readily the greater the distance between the two normal images. After the images move beyond the break points they rapidly come together and become more and more difficult to discriminate from each other. Accordingly, the inversion is more difficult to perform.

All of the paths lie in one plane. The jumping movement of the sound image, especially one that appears in the middle of the head, from the anterior to the posterior path, can serve particularly well in a determination of the inclination of the plane of the path. This inclination is measured by the use of a long rod that is rotated about an axis parallel to the line of the two ears and adjusted as closely as possible to the direction of the movement. Then the inclination can be obtained as that of the rod.

In measurements of the direction of sounds the rectilinear path is of great importance. Thus if the relation between temporal disparity and changes of direction needs to be determined it is difficult to use the anterior path, for exact determinations of direction here require a measurement of the angle between the medial plane and a line passing through the sound image and the center of the head. An estimation of this angle or its evaluation on a scale placed around the head is difficult, and it is even more difficult to locate the center of the head. Moreover, the

form of the anterior path varies greatly in different individuals and changes markedly with sound intensity. With the rectilinear path, on the other hand, these difficulties are absent. It is the same for all subjects, and its form is independent of loudness. Also most subjects can make precise judgments of the movements of the image along this path after a little practice in the estimation of distances.

The circuit of Fig. 8-9 was used to determine the shifting of a sound image along the rectilinear path. It consisted of two similar pairs of tubes which could be used to produce sound images independently of one another. If switch S_1 was switched to the upward position and S_2 to the next-to-the-lowest position, a tone was applied to the upper pair of tubes. If S_1 was switched to the second position, the tone was applied to the lower pair of tubes. If S_1 was turned to the third position, the tone was

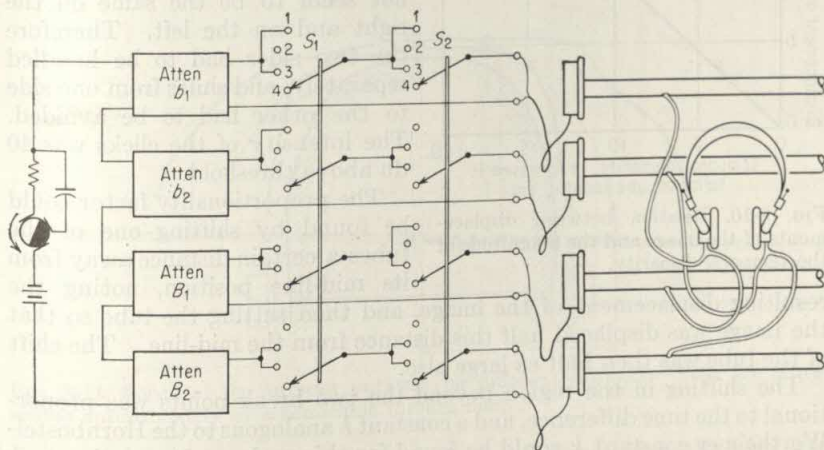


FIG. 8-9. Arrangement for the observation of two sound images.

applied to both pairs of tubes. Attenuators b_1 and b_2 or B_1 and B_2 were used to make a comparison of the loudness on the right and the left for each image separately, with S_2 at the two uppermost positions. Also B_1 and B_2 were set, with S_2 at one of the two uppermost positions, so that as S_1 was alternated between the two uppermost positions no change in loudness was perceived. Then the loudness of the two sound images was equal. It was necessary to have the correct polarity of the phone.

Now the upper and lower tube systems were adjusted so that the two sound images seemed exactly at the mid-line. Then the lowermost tube was shifted a certain amount Δt so that the lower sound image moved to one side. By switching S_1 to the two uppermost positions, with S_2 at the next-to-the-lowest position, now one and now the other image came in, so that it was possible to obtain reliable indications on a scale which represented the same distances as the movements of the image. As a test of the precision with which the shifts were judged, the image was made to shift from the mid-line to the break point and was compared

with the sum of the two shifts, one from the mid-line to an intermediate position and another from here to the break point. In these measurements it was convenient to operate S_1 automatically at the rate of once per 5 sec.

Figure 8-10 shows for several subjects the mean values of the shifts of the image corresponding to various time differences. The time differences are shown relative to a mean time difference at the break point of $\Delta t = 15$ cm. There is an obvious proportionality between the two

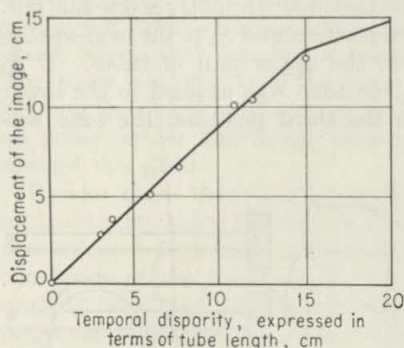


FIG. 8-10. Relation between displacements of the image and the magnitude of the temporal disparity.

resulting displacement of the image, and then setting the tube so that the image was displaced half this distance from the mid-line. The shift of the tube was then half as large also.

The shifting in the region beyond the two break points was proportional to the time difference, and a constant h analogous to the Hornbostel-Wertheimer constant k could be found for this region. Its relation to k was found by comparing the shift from the break point to the extreme lateral position with the shift from the mid-line to the break point. For a tone 40 db above threshold the mean value of $h = 0.35k$.

A few individual values of the ratio h/k for several subjects are as follows: 0.32, 0.39, 0.44, 0.27, 0.37, 0.32.

The results were less precise when the sound intensities were greater, because the sound image became vague and the displacement could no longer be estimated exactly. As a test of the accuracy of the measurements of displacement the displacement from the mid-line to one extreme lateral position was measured. This value must be equal to the sum of h and k .

The circuit of Fig. 8-9 was used to determine exactly the time difference between the extreme lateral positions. For this purpose the two tube systems were adjusted for equality of loudness, and then a large time difference $\Delta t > 2k$ was produced. Then the time difference of one system was reduced to a value at which a displacement of the image was still just imperceptible when S_1 was operated. It was essential here that the timbre of all four phones be absolutely the same. By this method, all

subjects were able to observe that the extreme lateral position was reached when $\Delta t = 2k$.

To obtain a picture of the measurements of the anterior path of the image for various subjects the loudness was chosen so that the image was in front and outside the head in the immediate vicinity of the forehead. To find the distance from the skin a small scale was placed perpendicularly on the surface of the head, and an attempt was made to indicate the distance by moving the thumb along the scale. This procedure worked well when the distances were small.

To obtain the distance of the lateral position from the head, a wire was bent to conform to the head and placed in the plane of the sound path. Then, with the loudness held constant, a certain time difference was introduced, a scale was moved along the wire to the position taken by

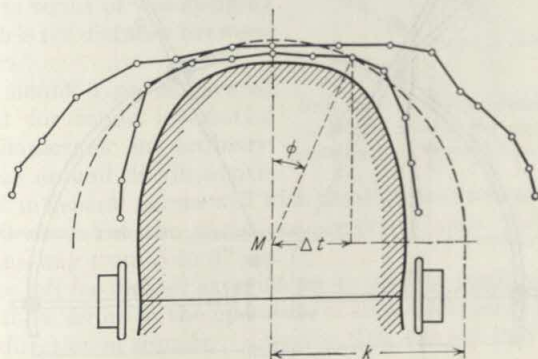


FIG. 8-11. Forms of the anterior pathway for different subjects. They are represented approximately by a semicircle (broken line).

the image, and as before the perpendicular distance from the wire was indicated. When the perpendicular distances from the wire had been found for a number of points, the form of the wire was recorded as in Fig. 8-11, and from the distances observed a continuous curve was drawn representing the form of the sound path. This method gave the path in good reproducible form. In the figure the axis of the ears runs through the two phones.

It was found that the two indicated paths, which were the closest and the most remote that were found, had a mean value that could be represented as a semicircle with its mid-point M approximately in the center of the head. It was further found that jumps from the rectilinear path in a forward direction ran nearly perpendicular to this path, and also that the shifting of the image along the path was proportional to the time difference. It follows that the relation $\Delta t = k \sin \phi$ between the directional change ϕ and the time difference Δt as expressed by Hornbostel is approximately valid. Here k is the time difference for the break point.

A test of the form of the sound path was made by introducing small changes in the time difference for some given position of the wire form

and trying to find the direction in which the sound image moved. It was often possible for a rod that could be rotated in the horizontal plane to be placed parallel to the direction of movement. The measurements of this direction must coincide with the tangent of the sound path. Precise values were obtained only when the tubes were shifted by extremely small amounts.

In these observations it was necessary to be sure that the loudness was the same in the two ears. An inequality produced an asymmetric distortion of the sound path.

The mid-point of the semicircle that was used to represent the anterior sound path agreed well with the center of the head as ascertained by other psychophysical methods. The arrangement of Fig. 8-12 was used to

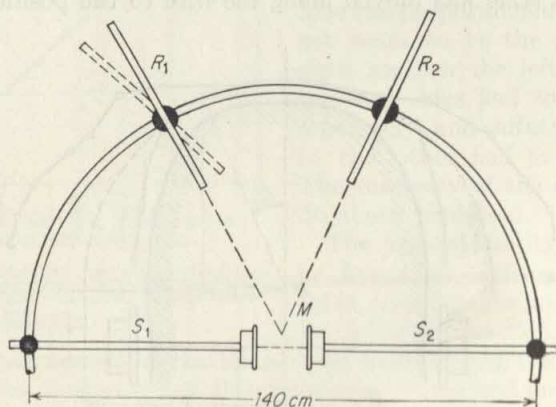


FIG. 8-12. Arrangement for determining the center of the head.

determine this point in relation to the axis of the ears. The two bars S_1 and S_2 were fastened to the head so as to lie in the axis of the ears. Tubes R_1 and R_2 could be rotated about a vertical axis in a plane located about 10 cm below the axis of the ears, so that their directions could easily be observed. When these tubes were rotated back and forth until they gave the impression of going through the middle of the head, a well-defined sensation arose. Thereupon the tubes were lengthened by sliding some fitted rods through them up to the point of intersection, and this point was found to lie at an average distance of 4.5 ± 1 cm in front of the axis of the ears.

In this determination of the center of the head the main role is played by the visual space system. The center of the system nearly coincides with the center of the semicircle for moderate intensities of sound. Yet the center of the semicircle is not the center of auditory space, for if this were the case a sound presented in one ear only, whose image lies on the axis of the ears a few centimeters inside the head, would seem to come from the back, and this is not so. It therefore seems that when the sound image jumps from the anterior to the posterior path, the deflections of the image from the middle plane are increased, as shown in Fig. 8-13.

The reason for this is that the posterior path is only a short distance from the axis of the ears on which the center of auditory space seems to lie.

These variations in the center of auditory space from the center M of Fig. 8-11 and the uncertainties that arise from individual differences in the circularity of the sound path are manifested as a failure of the equation $\Delta t = k \sin \phi$ to give actual angular displacements. Still, the difference between the actual plane of incidence of the sound waves and the one indicated by the observations is only slight compared with the difference between k (expressed in terms of wavelength) and l , which is the distance between the two ears.

It is no doubt a providence of nature that for sound intensities that are important in ordinary affairs, those around 40 db above threshold, k in general agrees well with the distance between the two ears of about 20 cm. Yet the variations are often large, and k may have values all the way from 5 to 37 cm.

It must be left for further experiments to disclose what factors serve to correct for these errors in the operation of time differences in the perception of the direction of sounds. Actually, they are not fully compensated for.

If continuous tones were used instead of clicks, there was a significant loss of accuracy in the perception of the direction of sounds, though the experiences had the same character for wavelengths λ greater than $2k$. For two wave trains of the same frequency (representing the stimulation of the two ears by a continuous tone), the maximum displacement of the sound was found when $\Delta t = \lambda/2$, and an increase in the time difference led to a smaller displacement of the sound to the opposite side. When $\Delta t = \lambda$ nothing was observed, since in this case there was no difference between the wave trains at the two ears.

When $\lambda/2 < k$, the maximum obtainable time difference was not sufficient to displace the sound image as far as the break point, and so the image could only be observed in the middle portion of the sound path. Theoretically it is of great importance, as Hornbostel pointed out, that a frequency for which $\lambda/2 = k$ gives a sound image that just reaches the break point. This fact indicates that the waves of excitation that pass along the two auditory pathways of the nervous system must have the same periodicity of variations as the tone itself. Actually the waves of excitation would be expected to have a periodicity twice that of the tone. Then the conditions would reflect themselves for every time difference equivalent to $\lambda/2$, and the most extreme lateral displacement would be reached for $\Delta t = \lambda/4$.

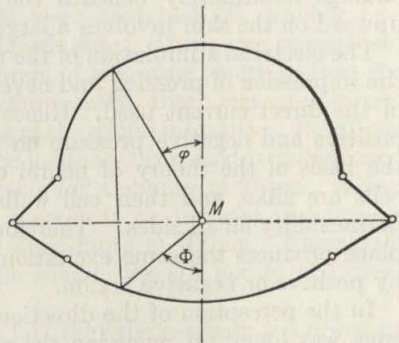


FIG. 8-13. Relative deflections from the middle plane for the same sound in the anterior and posterior pathways.

It is known from the study of pressure sensitivity on the skin that a depression and an elevation of the skin cannot be distinguished if care is taken to excite the same nerve endings. Ordinarily these two forms of stimulation can be differentiated because a depression excites only those endings immediately beneath the stimulating object, whereas pulling upward on the skin involves a larger area, though at lower intensity.

The electrical stimulation of the nerve endings of the skin always gives the impression of pressing and never of pulling, regardless of the polarity of the direct current used. Hence the neural excitation is the same for positive and negative pressure on the skin. This is to be expected on the basis of the theory of neural excitation (see page 232). All nerve cells are alike, and their cell walls have the same characters of semi-permeability on all sides. Therefore an increase in concentration at one place produces the same excitation regardless of whether it is produced by positive or negative action.

In the perception of the direction of a sharp click no important difference was found on reversing the polarity of one of the phones. Some subjects were unable to detect any differences at all, though others perceived the sound image as larger and more poorly defined. Yet the break points could be located in the same manner in these two situations. A reversal of polarity caused a shift of the mid-point, varying in direction and amount in different subjects, and apparently depending largely on the ossicular chain. This chain perhaps does not act in exactly the same way in response to positive and negative deflections.

The old idea that the basilar membrane is only stimulated once in each period of the stimulating sound, namely, when the hairs of the sensory cells strike against the tectorial membrane, cannot be regarded as valid. The nerve endings in the cochlear duct are surrounded by elastic tissue and by fluid of high viscosity. Consequently there are positive and negative effects for all vibrations of the basilar membrane. This will certainly be true if the tectorial membrane is attached to the cells that surround the nerve endings.

Because the excitation is the same for positive and negative pressure there will be two maximums of excitation during each period of the sound. Hence there will be a doubling of the periodicity. This doubling can be avoided if along with the oscillations of pressure there is a static pressure, which is increased and decreased by the oscillations. It is likely that a static pressure is produced by the fluid eddies. When the tone is turned off, this pressure ceases, so that there is no persistent excitation.

After stimulation with a tone has reached a steady state the movements of the basilar membrane at the different locations will vary in phase. Yet this variation is of no importance in the perception of direction, for the combining of the neural effects from the two ears is such that corresponding locations on the basilar membrane with the same phase will interact.

Interaction of Two Sound Images of Equal Loudness. When the circuit of Fig. 8-9 was used to produce two sound images of equal loudness and switch S_1 was set at its next-to-last position so that the two

images were produced simultaneously, the two images usually fused to one whose direction is now to be considered.

The first question is whether two clicks, which in this instance occurred in rapid succession, are capable of independent transmission to the nerve endings by the eardrum and ossicles. To test this point, two of the phones, say, the second and fourth, were switched off, leaving two successive clicks to be presented on the left side. If the two phones had the same polarity and the two tubes were of the same length so that the two clicks reached the eardrum simultaneously, there was an increase of loudness corresponding to a doubling of the sound intensity. But if one of the tubes was changed in length, the loudness decreased strikingly and on the average reached a minimum value for a change of 21 cm. When the tube length was further altered there was an increase in loudness until the original value was reached once more at 42 cm. Thereafter there was a further weakening of the sound, though not to the same extent as before.

These phenomena depend upon the fact that the eardrum is a resonant system with a natural frequency of about 800 cps and with moderate damping (Tröger). When exposed to a series of damped waves, as in a click, all these waves are involved in producing the loudness that is perceived, because a complete building up of loudness requires more time than the action time of one single damped wave, so that several of the damped waves add up in the action. If there is a time difference between two successive clicks equal to half the periodicity of the natural vibrations of the eardrum, which is about 21 cm of wavelength in this instance, the vibrations are largely canceled, and there is a reduction of loudness. This effect recurs periodically for a tube distance of 42 cm. As the time difference is increased the reduction of loudness becomes less, because the cancellation effect is taking place for a smaller number of vibrations. The adjustments of the tubes by which the loudness changes are produced are independent of the intensity of the clicks.

The direction in which the fused click image is perceived is somewhat modified by these effects of the eardrum, but the character of the image is not altered. If the change in loudness is great, it must be produced by transient vibrations of the telephone diaphragm and not by the eardrum.

The circuit shown in Fig. 8-9 was adjusted by using S_2 and operating all the phones with the same polarity so that the loudness was equal in the two ears for both tube systems. Then each pair of tubes was set in such a way as to give a sound image in the mid-line. When both systems were switched in at the same time the fused image remained in the mid-line. This did not occur when one of the images was displaced relative to the other, as could be done by changing the length of both tubes of one pair by the same amount.

One pair of tubes was adjusted to give an image at the break point on one side and the other pair was adjusted to give an image at the break point on the other side. Then when one of the pairs of tubes was altered in length the fused image moved from one break point to the other, just as in ordinary perceptions of sound direction. Hence the temporal

distance between the two break points was the same as in ordinary directional hearing, and there was nothing in the situation to show that a fused image was present. Moreover, the displacements of the fused image were proportional to the adjustments of the pair of tubes. If the two images were not located at the break points of the sound path but were placed a short distance from the mid-line and were symmetrically situated on the two sides, the fused image moved continuously from one of these positions to the other as the length was altered for one pair of tubes. The necessary variation in the tube length was again $2k$.

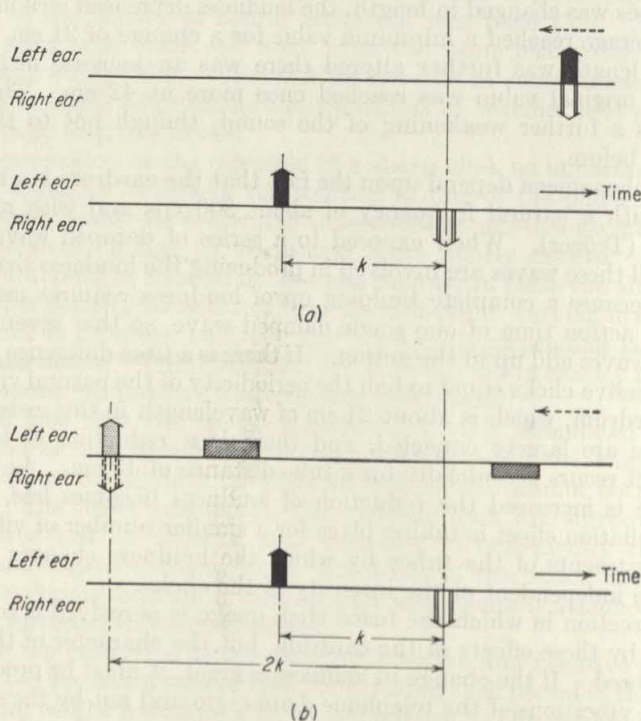


FIG. 8-14. Schema to show the temporal relations between a sound image in the mid-line and one at the break point.

The precise temporal relations between the addition of a sound image in the median plane to one situated at the break point on one side are shown in Fig. 8-14a. Here each click is represented by a large arrow on the time line, a black arrow for the left side and a white arrow for the right. The upper time line relates to the upper pair of tubes, in which the two clicks were applied simultaneously so that the sound image appeared in the middle. In the lower pair of tubes the click on the left appeared earlier, and the sound image was perceived on the left side. When both systems were switched on together, the image was perceived

on the left at the break point, because the median image appeared relatively late and was masked by the lateral one. When the median image was displaced, as indicated by the dotted arrow, the fused image remained on one side until the temporal separation of the two clicks on the left (indicated in black) amounted to $1.5k$, when it began to show a displacement. This process was continued in regular fashion until the displacement reached $2k$, and from there on the image remained in the middle, because then the middle image was the first to appear and it masked the lateral one.

Ordinarily the beginning of the movement was sharply perceived and reproducible, and so was the end when the displacement reached $2k$. This was not always the case because the middle image could be made prior by a considerable amount without any movement being produced, and then suddenly, without any outside influence, it jumped to the position that it would have occupied by the regular form of movement. After a little practice most subjects were able to produce or to prevent this jumping voluntarily. In Fig. 8-14*b* the crosshatched rectangles represent the temporal regions in which it was usually easy to produce a jumping back and forth of the fused image by a temporary inhibition of one image. If the middle image was moved into the crosshatched rectangle at the upper right, the sound image moved from the break point on the left a little toward the middle, whereas for the crosshatched rectangle on the left the image jumped from the middle toward the left. There were no loudness variations when these jumps occurred, but the character of the image was somewhat altered, though only to an extent corresponding to the change of direction. In the region between the two crosshatched rectangles the image moved in a perfectly regular fashion.

This obscuring of certain phenomena produced by a wandering of the attention was especially common when the subject concentrated upon one experience and the other was introduced gradually. The effect is well known in psychology. It always occurs when several items are perceived at the same time. Sometimes a grouping of the items is not possible, and one or several of them are left out. Whenever the compound is familiar, certain items necessary for its completion may be supplied voluntarily. Thus Stumpf (4) noted that, in the synthetic production of speech sounds, when the correct intensity relations of certain tonal components have not quite been obtained, the complex nevertheless takes on the character of a speech sound, though soon afterward the composition disintegrates of itself.

In the experimental situation, where sound directions were established by means of time differences, the sound image was always perceived at a particular distance from the head, depending on the sound intensity. In actual hearing, the distance of the sound is determined by other conditions, and the components discussed above are suppressed.

The extent to which particular components can be enhanced or suppressed through familiarity with a phenomenon is best indicated in measurements of intelligibility in a communications system. If verbal

material is broken up into isolated syllables a serious distortion will result in a false understanding of as much as 30 per cent of the syllables, whereas if the material is presented as continuous text it will be perfectly comprehended.

Familiarity has the further effect of making it difficult to acquaint a person with a new combination of elements after he has already experienced these elements in another form.

When a noise is heard and is located to one side the direction seems precise and unitary, in spite of the fact that the low frequencies in the noise have a different direction from the high frequencies and always fall in the mid-line. Thus there must be several neural centers that determine the direction, and all of these determinations are finally brought into line by a higher center.

In favor of this view is the phenomenon of suppression, as just described, for only in this way is it possible to account for the fact that certain directions are ordinarily left out of consideration in the complex. It would be difficult to understand this sort of suppression if the directions themselves were not fused but instead the fusion came about by the convergence of the first two excitations to produce a single direction, thus altering the magnitude of the excitation in the two ears. In this connection it is clearly necessary that the various excitations shall at the outset be directed into the proper neural channels. This is possible, because a certain neural set is always present during the listening to a series of clicks. It is especially desirable to present one image first and then to bring in the second, for then it is possible to suppress one or the other.

If the two images are presented simultaneously and are made equal in loudness, then it is common to perceive a fused image in the middle between the usual two images. If the two are not simultaneous, then the second will be suppressed in exactly the same way that in ordinary directional hearing the second of two stimuli in the two ears is suppressed. There is complete suppression if one of the images leads the other by the interval k .

Consequently the two directions represented in different nerve centers are united in the same way that the excitations in the two ears are. Moreover, this sort of fusion of excitations seems to be a general characteristic of the nervous system and not one peculiar to the perception of the direction of sounds. Klemm described the same sort of phenomena for pressure on the skin.

In order to obtain the relative latencies of the different kinds of sound images, a special schema will now be developed. Thus it is possible that after certain neural elements are excited an effect remains for a time, and during this time another impression cannot be received. Thus we can conceive that the characteristic of direction arises when the excitation produced in one ear passes through a certain sharply restricted region of the nervous system at a final rate and tunes up the cells there to the particular direction. If all the cells of the region are tuned up by stimulation from one ear, the sound image is perceived in its extreme lateral

position. This occurs if the sound in one ear leads that in the other ear by $2k$. If the two sounds are applied simultaneously, the group of cells is affected in different ways by the two excitations, and the two excitations fall in the middle of the cell group, whereupon the transmission of the excitation stops and the cell group can transmit its directional relation to a higher zone. The upper sketch of Fig. 8-15 represents the relations when the excitation in the right ear, shown by the white area, is earlier by 2δ than that in the left ear, shown by the black area. Accordingly the point of contact of the excitations on the two sides is displaced from the middle by δ .

Let us further assume that the displacement of the sound image from the mid-line along the rectilinear path can be determined by the excess of stimulated cells on one side relative to the other, as compared with the total number of stimulated cells. Then from the lower sketch of this figure, where the excess is represented by the crosshatched area, we can see that the displacement from the mid-line increases in proportion to the time difference up to the point where $\delta = k/2$. For this displacement, which corresponds to a time difference of $\Delta t = k$, the crosshatched area has spread so far from the middle on both sides as to occupy the whole elevated portion of the figure. From this point on, the displacement of the image slowly increases, because a given extension of the crosshatched area slowly increases its area until for a displacement of $\delta = k$ (resulting from a time difference of $\Delta t = 2k$) there is no further displacement. When we consider the limited displacement beyond the break points, represented here by making the height 0.35 of that in the middle, then the shifting of the image corresponds exactly to what is observed.

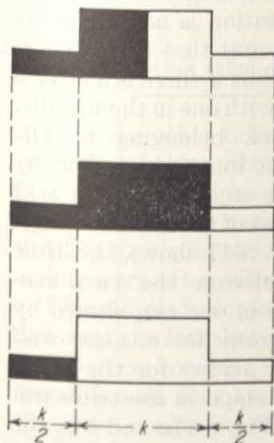


FIG. 8-16. Forms of bilateral excitation for different directions of a sound.

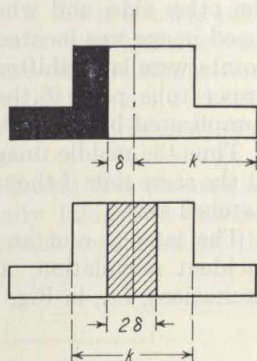


FIG. 8-15. Schema showing the bilateral stimulation of cell groups that determines sound direction.

In Fig. 8-16 are represented the different bilateral conditions of excitation corresponding to the location of the sound image in the middle, at the left break point, and at the right break point.

It is apparent that when the image is in the middle it can be displaced to one side by a time k , reckoned from the beginning of excitation of the group of cells, whereas an image at one of the break points requires $\frac{3}{2}k$ from the beginning of excitation. The difference of $k/2$ could be verified experimentally, for, as shown in Fig. 8-14, the region in which jumping occurred was sym-

metrically disposed about a point that followed the application of the first click by $k/2$ for the lateral image.

When the lower pair of tubes was used to locate one sound image at the break point on one side and the other image was located at this point on the other side, and when by adjustment of the upper pair of tubes the fused image was located at the break points, it was found that the break points were later shifted by $k/2$, relative to the first incident click of the upper tube pair, if the lateral image in the upper pair of tubes was complicated by the presence of a central image.

Thus the middle image and the lateral image at the break point arose at the same time if the middle image of Fig. 8-14 was located at the cross-hatched axis.

The latency τ of an image of any direction depends upon the first incident stimulation, and is given by the meeting point of the two excitations, *i.e.*, in Fig. 8-15 by $k + \delta$ where $\delta = \frac{1}{2} \Delta t$, hence

$$\tau = k + \frac{1}{2} \Delta t$$

A simple fusion of the directions of the images occurs if they arise at the same time, for then there is no mutual suppression. When the

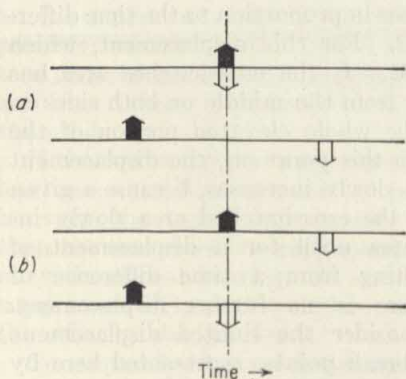


FIG. 8-17. Schema showing that the fusion of two equal and simultaneous images is equivalent to a single image halfway between the two.

remaining extent of the two excitations is equal to the total length of the cell group, the moment at which the excitation appears over the whole length remains the same if the one excitation is advanced by the same amount that the other is retarded. Thus if there is a lateral image along with one in the middle, the first click belonging to the lateral image must be earlier by $\Delta t/2$, and the second must be $\Delta t/2$ later than that of the middle image. Then, as Fig. 8-17 shows, the time difference between the two successive clicks in one ear, shown by the black arrows for one ear and by the white arrows for the other ear, must be equal in the two ears.

The chronological order of the various clicks in Fig. 8-17a and b is the same. If we use the obvious law that two images with the same direction do not show any change of direction when they fuse, then this will not be true if they do not arise at the same time. When there is mutual suppression of the image no change of direction appears; hence the two figures show that the fusion of two equally loud and simultaneous images can be regarded as a single image halfway between the two. Accordingly the time difference between the two equal images in Fig. 8-17b is equivalent to the mean of the two time differences in Fig. 8-17a.

To test this point experimentally, the two sound images were given the same temporal characteristics by adjusting the two tube systems (as shown in Fig. 8-9). To do this the two inside tubes (for example) were switched out, and the remaining pair of tubes was adjusted as necessary to bring the sound image to the mid-line. Then if the two inside tubes were switched in once more the upper and lower tube systems were adjusted to give an image in the mid-line. Hence all four stimulations were simultaneous. If then, proceeding from this setting, one tube of a pair was lengthened by the same amount that the other was shortened, the temporal equivalence was maintained.

The measurements were carried out by introducing first the median image, then adding the lateral image, and finally taking the median image away. The resulting shift depends upon the separation of the two different images, as shown in Table 8-2.

TABLE 8-2

Subjects	Shift from the mid-line to the combined image	Shift from the combined image to the lateral image
1	0.533	0.400
2	0.536	0.462
3	0.502	0.571
4	0.500	0.598
5	0.462	0.540
6	0.538	0.432
Mean value	0.512	0.499

If in the other tube system also one tube was lengthened by the same amount that the other was shortened, two simultaneous images appeared at certain directions and united to form a single image in the median plane. Still, the variations were usually limited to one side, because the displacements on the two sides necessary to produce the same time variations were often different.

This simple fusion of images can occur also when the images are slightly different, as Hornbostel has shown.

When we consider the fusion of two images whose temporal conditions are different, four types are possible. Thus it may happen that one of the two images is completely obscured; this happens when it arises earlier than the other. Then when there is a simultaneous shifting of the upper and lower tube systems no change of direction occurs, although the timbre is altered somewhat. The appearance of this phenomenon is favored if one of the images is made weak and its intensity is gradually raised to the point of equal loudness. The two types of phenomena that appear in this procedure are represented by the black dots in the two uppermost diagrams of Fig. 8-18 for the fusion of a medial image and one at the left break point.

It was found also that the two pairs of clicks could be combined in two different ways to form two sound images, as already shown in Fig. 8-17*a* and *b*. The appearance of one combination or the other could be favored by shifting the two clicks together or moving them to and fro. If there was no noticeable difference in timbre between the two clicks, this procedure worked well, though not in every trial. For the most part the transition from one type to the other occurred suddenly, without any particular reason. It was often helpful to vary the timbre of the two clicks by inserting condensers in parallel with the phones. Then after the preliminary adjustments of the circuit had been made these condensers were gradually reduced in value.

If the click was heard in the manner indicated in Fig. 8-17*a*, the fused image moved from the left break point toward the mid-line and then stayed

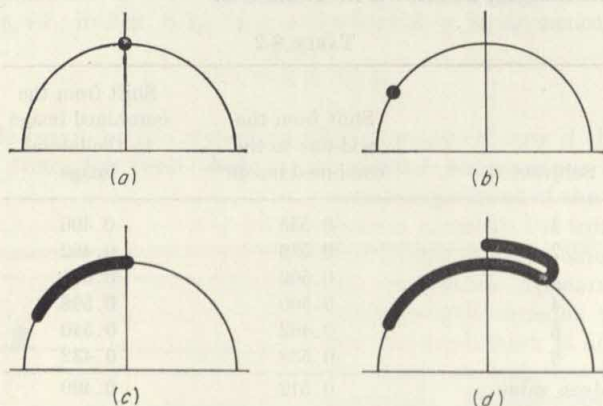


FIG. 8-18. Types of fusion of two sound images.

there. But if the perception was that indicated in Fig. 8-17*b*, a shifting of the upper pair of tubes caused the image to move through the mid-line to about half the distance of the break point toward the right and then turn back toward the middle and stay there. In order for the fused image that was going away from the mid-line to be turned around so as to approach it once more, it was necessary for the upper pair of tubes to be shifted by an amount approximately equal to k . These two types of phenomena are represented in Fig. 8-18*c* and *d*.

The displacement of the combined image on the right side, which at first seemed incomprehensible, can readily be explained if in Fig. 8-14 we consider the medial sound image of the upper pair of tubes in the left position as indicated by the crosshatched arrows. In the fusion as represented in Fig. 8-17*b*, one sound image, produced by the middle pair of tubes, appeared at the break point on the right side, and another image appeared at the extreme lateral position on the left. As may be seen in Fig. 8-16, the extreme lateral image arose later, by the time $k/2$, than the image at the break point did. Hence it partly obscured the image on the left, and the fused image appeared on the right. If the

upper pair of tubes was shifted further, the time of appearance (latency) of the left image was not altered further, because it followed the appearance of the first excitation by the time $2k$, and the whole group of cells was affected. For the image on the right, however, the latency increased from $1.5k$ (for a tube shift of $0.5k$) to the same value of $2k$ as for the left image, so that then there was no mutual obscuring of the image and the combined image appeared in the mid-line.

The nature of the combination of clicks can be judged to some extent by the timbre of the fused image. If the median image obscured the lateral one, the fused image seemed brief and impulsive. On the other hand, if the form of perception was that of Fig. 8-17*b*, the image seemed diffuse and not so impressive.

It was found that two images at the most extreme lateral positions on the two sides of the head could be altered by simultaneous adjustments of their temporal relations in just the same way as may be done with two uniaural images. This fact indicates that so far as directional hearing is concerned there is no difference between an extreme lateral binaural image and a uniaural one.

A uniaural image was produced by switching off one of the phones shown in Fig. 8-9, and simultaneously a binaural image was presented at the extreme lateral position. When the unilateral image was temporally displaced, the results were exactly the same as in ordinary directional hearing. The fused image appeared in the mid-line if the first two clicks were presented simultaneously to the two ears.

The only phenomenon that could not be observed without difficulty in the fusion of two images was the displacement of the images beyond the two break points. This is true because the combined image is significantly larger and less precise in its boundaries than the image experienced in ordinary directional hearing for faint stimuli.

Image Displacements for Unilateral Changes of Loudness. If with the arrangement of Fig. 8-1 the sounds to the two ears were made equal in loudness and the tubes were adjusted so that the sound image was exactly in the mid-line, then a gradual increase in sound intensity in one of the phones produced a continuous displacement of the image from the mid-line to the side where the intensity was the greater. As the disparity in loudness was increased, the image moved farther to one side until finally it was completely lateralized and was indistinguishable from a uniaural sound. The transition from a binaural sound image to a uniaural one was difficult to observe, because as the loudness disparity increased the image increased in size and lost its sharp contours. Then the smaller displacements from the median plane were difficult to perceive. This continuous displacement of the sound image with increasing loudness disparity was found in all subjects if care was taken that no alteration of timbre accompanied the intensity changes, and if the two clicks seemed alike in all respects on the two sides. Often it was sufficient to make the two phones alike, but account had to be taken of any differences in the acuity of the two ears. The variation of the threshold with frequency had to be considered, and any inequalities of the two ears

were compensated by introducing the proper amounts of attenuation at the phones.

Yet even when the clicks had been made exactly equal in the two ears, the image often did not move steadily away from the mid-line, but as the disparity of loudness was increased gradually, the image first remained in the mid-line and then suddenly jumped over to the proper position. Much the same thing happened when a click was introduced into one ear and then the other ear was stimulated with the same click at an intensity that was gradually raised above threshold. The image was perceived on one side for a time, and then it jumped to an intermediate position. For the most part, however, this suppression of the weaker unilateral image did not occur, and the image moved continually away from the mid-line from the very beginning.

If an intensity change led to an alteration of the timbre, or if the effects of the sound were different in the two ears, then an increase of sound intensity on one side finally produced a splitting of the image. This splitting might be complete or partial. On the side where the intensity was the greater a uniaural image was perceived, and in addition there was a binaural image whose position varied with the loudness disparity.

The question arises as to how the displacement of the image comes about when the intensity is increased on one side. First of all, it is possible that the velocity of nerve conduction depends upon the sound intensity, and in this way an intensity increase produces a time difference between the two excitations. However, this factor cannot operate for conduction within the group of cells that serves for the determination of sound direction, because as the loudness increases the velocity of transmission may become smaller; the time $2k$, which is necessary for the alteration of the entire group, increases with the sound intensity. Hence, in general, the stronger stimuli come in later and lose their effectiveness. Actually, it was indicated that for subjects with nearly constant k the same unilateral increase in sound intensity produced larger lateral displacements than for subjects with variable values of k .

Hence we can only be concerned with changes in the velocity of nerve conduction along the path from the basilar membrane to the cell group that determines the perceived direction. Now it is known that no change of direction is perceived for time disparities in tones above 3000 cps. For these tones the sound always remains in the mid-line, as long as the loudness is equal in the two ears. Hence a change of nerve velocity cannot have any effect upon the direction. For a click, on the other hand, a change in the latency of the nerve endings and of velocity of conduction has a significant effect upon direction. The voltages of the oscillators of Fig. 8-1 were chosen so that when switch S was operated there was equality of loudness for three types of sounds: a tone above 3000 cps, a noise, and a click. Then a median range was obtained for equal bilateral stimuli. When the sound intensity was raised on one side by adjusting one of the attenuators, practically the same displacements of the image were observed for all three types of sound.

Hence the changes of direction produced by loudness disparities are not to be attributed to the production of time disparities. Rather, they arise directly from relations of magnitude of the excitations.

This fact could be demonstrated particularly well by the use of a tone above 3000 cps that was modulated at a rate of 100 per second. For this purpose the circuit of Fig. 8-19 was used. The oscillator G_2 worked into the two attenuators b_1 and b_2 , and switch S was used to set up equality of loudness in the two ears. Oscillator G_1 , whose frequency was about 100 cps greater than that of G_2 , was allowed to beat with G_2 to give a beating tone whose amplitude variations (the degree of modulation) could be adjusted separately for the two ears with attenuators B_1 and B_2 . The bridge circuit, in which Z was made equal to the impedance of the attenuators, was used to prevent any interaction between the two oscillators.

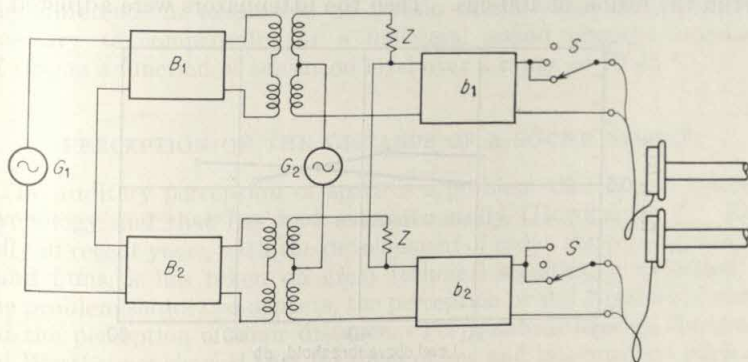


FIG. 8-19. Arrangement for observing changes of direction in beating tones.

If the modulation was gradually increased in the two ears in the same manner, a value was reached at which most subjects clearly perceived an unmodulated tone that remained in the mid-line, and at the same time they heard a completely modulated tone whose location varied according to the tube length. A few subjects did not experience any splitting of the image but observed a single one that with increasing modulation (for a constant time disparity) moved ever farther away from the mid-line.

If then the modulation was increased a certain amount in the left ear, the modulated tone (for equality of time relations) moved to the left, while the unmodulated tone remained in the mid-line. If at this point the over-all intensity was reduced in the left ear by the same factor by which the modulation was increased, the modulated tone appeared in exactly the same place as before. The unmodulated tone then moved to the right. For subjects who were unable to separate the two tones, the tone first of all shifted markedly to the left, and then as the intensity was reduced it moved somewhat to the right.

If at first the over-all intensity was increased in the left ear, the modulated tone moved to the left. Then if the modulation was reduced on the

left by the same factor by which the intensity was increased, the modulated tone seemed again to be exactly at the mid-line. If there was no splitting of the image, there was still a little deviation to the left. This deviation became smaller as the modulated tone was made larger relative to the unmodulated one.

These studies show that the direction of a fully modulated tone is independent of the over-all loudness. It is only important that the amount of modulation be exactly equal in the two ears. The unmodulated portion of the experience then does not play any role, though the two portions truly are propagated as a whole to the locus where directional hearing is produced. It is there that the splitting up of the image may occur.

Attenuators B_1 and B_2 as shown in Fig. 8-19 were connected each to separate oscillators G_1 and G_1' and were given frequencies about 1 cps apart in the region of 100 cps. Then the attenuators were adjusted so

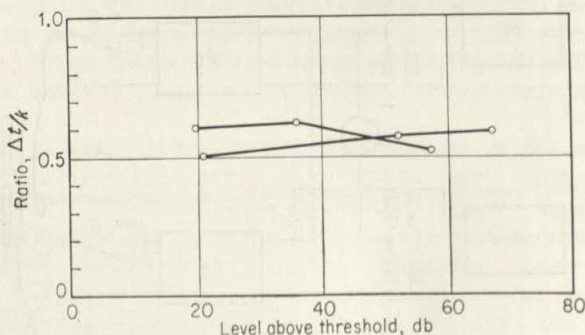


FIG. 8-20. Compensation for a time difference by means of an intensity difference, at various levels above threshold.

that the amplitudes of the beating tones were equal, and it was observed that when the loudness was equal in the two phones a regularly rotating tone was produced. This rotating tone was accompanied by a tone of 3000 cps that was beating at 100 cps, moving in a circle about the head. This tone had only a very small amplitude, so that a difference tone of 100 cps arising from the nonlinearity of the ear could not be large enough to reach the threshold of audibility. Also the combination of one tone of 100 cps and another of 3000 cps modulated by 101 cps did not produce a rotating tone. Hence the same neural elements that mediate 3000 cps must transmit these rapid intensity variations of the 100-cps tone, a periodicity that already possesses a tonal character. This fact is of interest in relation to the principle of specific energies of nerves (E. Meyer, 2).

It is thus established that for directional hearing with a unilateral increase in sound intensity the inequality in the magnitude of the excitations of the two ears is determinative, for in these instances, with the temporal relations in the excitation held constant, there must be considerably more cells in action on the side of the greater stimulation, up

to the place where the excitation on the two sides is combined. It is possible to compensate for the change in direction produced in this manner by giving priority to the weaker stimulus. If the priority is great enough that the same number of cells is involved in the two excitations, the sound image remains in the median plane.

It is now possible to determine the magnitude of the time difference that will compensate for a given unilateral intensity difference and the variations with the intensity of the excitation at the place where the effects in the ears are combined. Thus if the intensity in one ear is increased a given amount while the sizes of the regions of excitation in the two ears remain equal, the sound in the other ear must be advanced in time by an amount that is inversely proportional to the excitation. Results are given in Fig. 8-20 for two subjects for which the value of k did not change appreciably with sound intensity. The curves show the time difference Δt (expressed as a ratio to the value of k), which was necessary to compensate for a unilateral sound pressure increase of 8.7 db, as a function of sensation level over a range of 70 db.*

PERCEPTION OF THE DISTANCE OF A SOUND SOURCE†

The auditory perception of space is a problem that is well known in psychology and that has had extensive study (Hornbostel, 3). Especially in recent years, with the development of radio, the phonograph, and sound films, it has taken on great technical significance (Fletcher, 4). The problem shows two aspects, the perception of the direction of sounds and the perception of their distance. For binaural hearing Hornbostel and Wertheimer showed that for tones of low and intermediate pitch and for clicks the direction is determined mainly by the time difference in the incidence of the sounds at the two ears. For higher tones the direction is determined by binaural loudness differences. In ordinary telephonic communication systems these directional cues are absent, for they would require a separate transmission line for each ear. However, an impression of distance is present even for single transmission to one ear, and it contributes greatly to the lifelike quality of a sound.

A number of variables have been found to contribute to the perception of the distance of sound, yet it has not been possible to specify the physical magnitudes by which they operate.

Influence of Loudness on Sound Direction. The existence of a number of special physical attributes determining the perceived distance of a sound becomes obvious on listening to a sharp click and a continuous tone of 3000 cps in a moderately damped room. The sound image of the click seems small and sharply localized, and when the head is moved the source seems to remain stationary. On the other hand, the image of the tone is diffuse, and when listened to with one ear it seems to move

* [Here pages 865-868 of the original article have been omitted. They contained a theory of directional hearing based on the assumptions of Fig. 8-15.]

† Article 29 as listed in the Author's Bibliography. Published in 1938.

exactly as the head moves. For a continuous tone of 3000 cps there is no distance localization that is related to the actual distance.

A change in the loudness of the click has little effect upon its apparent distance. For the tone, however, despite the fact that an actual spatial localization is absent, an increase in loudness produces a clear reduction in the distance of the diffuse image. Thus it seems that loudness has an effect upon the perceived distance only in the absence of other more determinate physical cues.

Effects of Room Acoustics. In radio broadcasting it is well known that a listener in front of a loudspeaker can judge with considerable accuracy the distance of the speaker from the microphone (E. Meyer, 1;

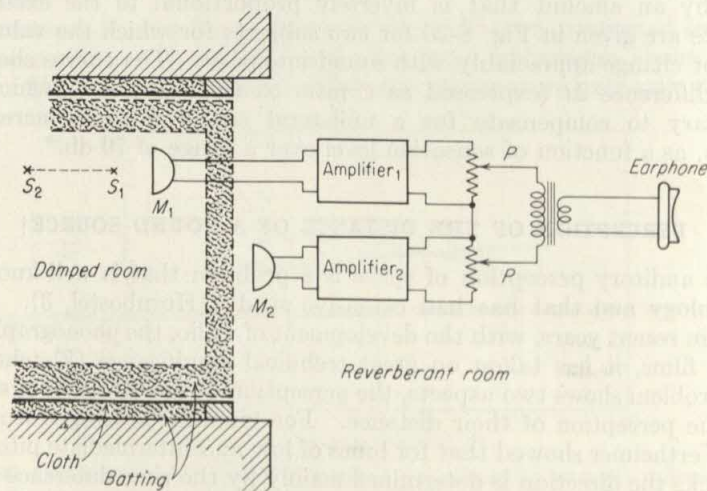


FIG. 8-21. Apparatus for the determination of perceived distance for various proportions of direct and reflected waves.

Maxfield; I. Steinberg and Snow; Rabinovich). The greater the distance, the more reverberant are the sounds and the farther behind the loudspeaker the sound image seems to be. This distance effect is further increased if the room is reverberant. The distance between the speaker and the microphone mainly affects the ratio between the sound reaching the microphone directly and that reaching it after reflection from the walls of the room. The perception of the distance of a sound in a room thus seems to depend upon this ratio.

To investigate these phenomena an arrangement was used as shown in Fig. 8-21. On the left is a small damped room that is separated from a large reverberant room by a layer of cotton 15 cm thick. So as to obtain a high degree of absorption of the low tones without making the cotton layer too thick, the walls were first covered with a sound-absorbent sheet and then the cotton layer was placed over this. As a result, the damped room gave practically a direct sound field. As this field penetrated the damping wall it encountered the undamped area, and there a prolonged reverberation arose. If the dividing wall was given

a sound attenuation of 20 db, the sound going back from the reverberant area into the damped room could be neglected. Hence to a first approximation the direct sound impinged upon microphone M_1 and the reverberant sound upon microphone M_2 . The two voltages were conducted through amplifiers to a potentiometer arrangement P that could be adjusted to give any desired relation of the two sound fields in the electrodynamic receiver. The two amplifiers were adjusted so that the two sound fields seemed equally loud, and also amplifier 2 was provided with a filter network that compensated for the frequency selectivity of the dividing wall.

If a speaker was stationed 10 cm from microphone M_1 and potentiometer P was moved downward, the loudness of the sound remained constant, but the component from the undamped room became greater. As a result, a listener had the impression that the speaker was moving farther away from his ear. Along with this increase in distance there was an apparent increase in the size or vibrating surface of the sound source, as indicated schematically in Fig. 8-22.

For the direct sound field the source seemed to be extremely small and to have great density, whereas the reverberant field had a more diffuse character.

The reverberant field consisted actually of reflection patterns arising at the walls. Because these reflections were at considerable distances from the sound source, the reverberant field also seemed well removed from the actual source. If now the direct sound field was made to overlap the reverberant field, then one field or the other became paramount according to the loudness relation, and a characteristic distance for the sound image was associated with each relation. Yet this sort of variation of the sound image does not represent a true perception of distance; it corresponds merely to a mixture of close and remote sound images both of which have already been determined by other cues.

Though this alteration in the ratio between direct and reverberant fields can indeed be used to produce the perception of a moving sound image, this ratio is not the basis of auditory distance. This is true because in a free space or in a completely damped room the sensation of distance is present and, in fact, is even more distinct and of much greater extensiveness than elsewhere. If in Fig. 8-21 the sound source is shifted to the position S_2 at a distance 40 cm from microphone M_1 , the listener experiences a much more definite displacement of the sound image in the

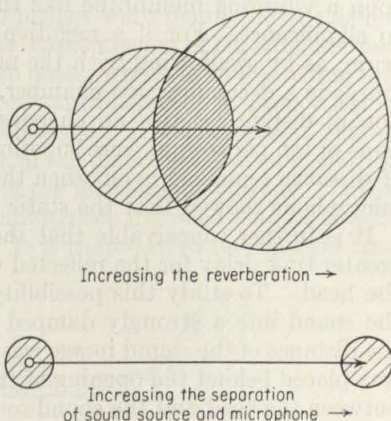


FIG. 8-22. The change in apparent distance when listening through a microphone system as the result of increasing the reverberation and increasing the separation of sound source and microphone.

receiver. Then, as the lower sketch of Fig. 8-22 indicates, the apparent size and density of the sound image remain constant, provided that the loudness is not changed.

Phenomena Giving Rise to Sensations of Distance. In the quest for the stimulating conditions giving rise to sensations of distance, it was first shown that the ponderomotive [static] forces that may be exerted upon a vibrating membrane like the eardrum by a sound source are of no significance. For if a negative pressure was exerted upon the eardrum, as by swallowing with the nostrils closed or by having the sound source in a decompression chamber, there was no reduction of the sensation of distance. Also no changes appeared when air-pressure oscillations of ten per second were superimposed. The fact that the sensations of distance remained even when the sounds were transmitted through a microphone showed that the static forces do not play any role.

It is further conceivable that the perceived distance depends upon a greater time delay for the reflected wave in its passage from the source to the head. To study this possibility a narrow tube was used to conduct the sound into a strongly damped room, and by listening with one ear the distance of the sound image was judged. If now a reflecting partition was placed behind the opening of the tube so as to enlarge the reflections between the head and the sound source, there was no effect as long as the sound intensity was kept constant.

It was more difficult to prove that the entrance of sound waves into the skull and their reception by bone conduction did not play any part. It was found that when the ears were completely occluded and the sound pressure was increased to compensate for the diminished acuity a certain degree of distance perception was still possible. This effect was especially convincing in a person whose external auditory meatuses were completely closed on both sides because of congenital deformations, though the ears were otherwise normal. Also the perception of distance could be demonstrated in some degree in persons who had lost both eardrums as a result of an operation. If the intense sound of an electric spark was listened to in a damped room when the ears were held closed with the fingers, there was a firm impression of a wave of pressure passing through the skull, and this was especially referred to the teeth.

The following arrangement was used to show that the sound field in the vicinity of the head is not necessary for the normal perception of distance, and that only those vibrations are important that enter the external auditory meatus. One ear, as shown in Fig. 8-23, was connected to a metal tube 100 cm long and 2 cm in inside diameter by means of an airtight rubber coupling. The other ear was closed. The metal tube was filled with loose cotton so as to prevent reflections and thus to give a simple traveling wave. It was found that on listening with such a tube the sensations of distance were present. The distance of the sound source from the end of the tube determined the perceived distance. It follows that the stimulus cues determining the perception of distance are transmitted through a damped tube without alteration.

If the sound source S_1 was approached with the end of the tube, the

sound source seemed to insinuate itself into the external meatus. Then when there was a further shift from S_1 toward the head it moved farther away once more. If the sound source was placed as close as possible to the head, there were two sound images, one corresponding to the distance of the source from the end of the tube and the other corresponding to the sound image obtained with both ears closed. By temporarily closing the end of the tube these two images were readily distinguished.

Effect of Microphone Stiffness on the Transmission of Directional Cues.

If the sound source is a radiator of zero order, which is an expanding and contracting sphere, then the sound pressure decreases in proportion to the distance and is independent of frequency. If a microphone acts as a pure pressure receiver, then a change in the distance between it and the source can affect only the magnitude of the microphone current. If this change is compensated for by amplification, then distance changes cannot affect the microphone current at all. It is therefore to be expected that

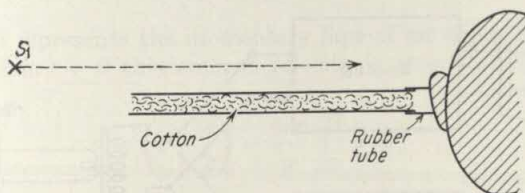


FIG. 8-23. Arrangement to prove that the sensation of distance is independent of sound intensity around the head.

for a microphone that acts as a pure pressure receiver there will not be any changes of apparent distance as long as the loudness is kept constant.

On the other hand, it is well known that a vibrating sphere produces a sound field in which the particle velocity of the air molecules has a phase angle relative to the sound pressure, and the size of this angle varies with the frequency and with the distance from the sphere. This is the only characteristic of the sound field that varies with distance, and so we may expect it to be the basis of distance perception. A transmission system must be able to reproduce the cues for distance to the extent that it can represent the velocity pattern of the sound field.

To study this problem, the arrangement of Fig. 8-24 was used. A telephone receiver M_1 with a heavy metal case of 5 cm diameter was fitted with an iron diaphragm of 0.8 mm thickness. Accordingly it had great stiffness when used as a microphone. A second microphone M_2 of similar form was fitted with a diaphragm as thin as possible, only 0.2 mm. On listening at the electrodynamic earphone and adjusting the two amplifiers for equal loudness of the sounds from M_1 and M_2 , it was found that sensations of distance were mediated by the less stiff microphone M_2 . However the sound image from the stiff microphone M_1 always seemed of a diffuse character and remained at the same place, as long as the intensity was kept constant. The difference between the two microphones was especially noticeable if the loudness was changed

by varying the amplification. The less stiff microphone showed little change of apparent distance, whereas the stiff microphone for the same variation of intensity exhibited a marked alteration of apparent distance. Here the distance at which the sound image was perceived depended merely on the loudness, and the normal cues for distance were absent.

It appears, therefore, that a sensitivity of the microphone to particle velocity is a necessary condition for its transmission of directional cues. Seemingly opposed to this idea is the observation that sensations of distance are still present when the ears are closed with the fingers. In order to give the microphone the same sort of stiffness that is given to the ears by closing them with the fingers, microphone M_2 was immersed in a large vessel of water to a depth of about 1 cm. The sensations of distance were still present, though somewhat reduced. It therefore

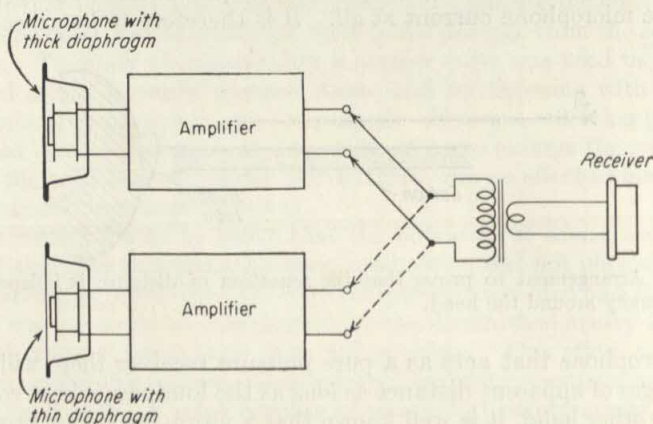


FIG. 8-24. Effect of microphone stiffness on the transmission of distance cues.

appears that the ear is able to make use of an extremely slight amount of velocity sensitivity.

Experiments with crystal microphones, which are sensitive to sound pressure only, showed an absence of distance perception when a single crystal was used. When a microphone was made of an assembly of crystal elements there was a limited perception of distance, perhaps because the framework containing the crystals was itself responsive to the particle velocity.

Difference in the Reception of Sound Pressure and Particle Velocity for a Divergent Wave. The relation between sound pressure and particle velocity is observed most readily for a vibrating sphere. In this class of sound sources we can include most loudspeakers and the human vocal apparatus when producing low tones, to a fair degree of approximation.

In a spherical sound field the velocity potential φ depends only on the time t and the distance r from the center of the sphere. The equation is $4\pi r\varphi = f(t - r/c)$, where $f(t - r/c)$ depends upon the boundary conditions and c is the propagation velocity of sound.

If ρ is the density of the air, p the sound pressure, and u the particle velocity, we can determine from the velocity potential the values $p = \rho \partial\varphi/\partial t$, and $u = -\partial\varphi/\partial r$. Hence the sound pressure is

$$p = \frac{\rho}{4\pi r} f' \left(t - \frac{r}{c} \right) \quad (8-1)$$

and the particle velocity is

$$u = \frac{1}{4\pi} \left[\frac{1}{cr} f' \left(t - \frac{r}{c} \right) + \frac{1}{r^2} f \left(t - \frac{r}{c} \right) \right] \quad (8-2)$$

The physical meaning of the function f is easy to determine. If we consider the mass of air that is displaced by the sound source per unit of time, we find at the point of origin of the spherical wave (at the center of the sphere) that

$$\lim [4\pi r^2 u]_{r \rightarrow 0} = f(t)$$

Therefore $f(t)$ represents the momentary flow of air from the source.

If at the time $t = 0$ this current velocity is zero, then Eq. (8-1) can be written

$$f \left(t - \frac{r}{c} \right) = \frac{4\pi r}{\rho} \int_0^t p \, dt$$

Then from Eq. (8-2) the particle velocity is

$$u = \frac{1}{\rho c} p + \frac{1}{\rho r} \int_0^t p \, dt \quad (8-3)$$

It is then obvious that the pressure contains only the first derivative of the particle velocity, but the particle velocity contains the function f also. The smaller the distance from the source, the more important is the function f . It is therefore to be expected that when a velocity microphone is used and listening is done with a receiver the ratio between the two terms of Eq. (8-2) may be altered by differentiating or integrating the microphone current. This ought to produce a change in the apparent distance of the sound image.

To investigate this possibility, the circuit of Fig. 8-25 was used. The current of a velocity microphone was conducted through the resistance-capacity network shown at the bottom of the figure. With switch U at its uppermost position an integration of the microphone current was obtained if condenser C_1 and resistance R_1 were made very large, and C_2 and R_2 were given the usual values of a resistance-coupled amplifier. When the switch was in its middle position there was normal amplification. When it was in its lowermost position there was a differentiation of the microphone current if condenser C_3 was given a small value.

Now the sound source was placed 50 cm from the microphone, and with the switch in its middle position the sound was adjusted to a comfortable loudness in the receiver. The image was then localized about

50 cm behind the receiver. At this distance the second term of Eq. (8-2) becomes very small. Now U was switched to its uppermost position so that there was an integration of the microphone current and an increase in the magnitude of the second term of Eq. (8-3) corresponding to a close approach to the sound source. In actuality the sound image in the receiver jumped from about 50 cm to about 8 cm from the ear.

On the other hand, if the sound source was placed about 5 cm from the microphone, then when the switch was set for differentiation the sound image in the receiver receded from about 5 cm to about 50 cm away. These observations held equally well for speech, spark sounds, and a rattling tone. For tones and clangs there were usually no variations of distance.

For successful results in this experiment it was necessary to have a well-designed transmission system. If any nonlinear distortion arose in

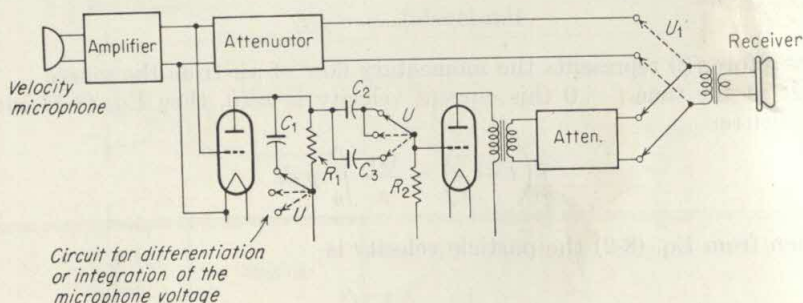


FIG. 8-25. Circuit for studying the effects of differentiation or integration upon distance cues.

the amplifiers, for example, the resulting overtones were almost invariably localized in the immediate vicinity of the receiver diaphragm, and any major alterations of apparent distance were lost. If the diaphragm of the receiver was not properly damped, the transients produced by a click were sharply localized at the diaphragm, which likewise was greatly disturbing. These possible errors were checked by listening with the switch U_1 set for direct transmission.

If a bone-conduction receiver was used instead of the receiver, the sensations of distance were still present if one ear was closed with the finger, thereby bringing the sound image to one side of the head.

No differences in the magnitude of distance effects could be observed for radiators of zero and higher order. This is to be expected, because most radiators can be regarded as a combination of two radiators of zero order acting in opposite phase.

Because a differentiation or integration of the signals has such a natural effect upon the distance phenomena, it seems that the important factors are the relative sizes of the two quantities $f(t)$ (the flow velocity) and its first time derivative. Therefore no true distance indication should be present for a flow velocity that is the same as its first derivative, $f'(t) = f(t)$. It is especially to be expected that no true distance will

be observed for pure sinusoidal tones, because the phase shifts that appear as a result of differentiation are not perceptible to a single ear. This is easily proved on listening to a continuous tone transmitted by a microphone. If the source and microphone are in a different room from the listener, it can readily be shown that the apparent distance of the sound is determined merely by the intensity in the receiver. For direct listening with one ear it is much more difficult to obtain clear results. If the proper distance cues are lacking, any other available one will unconsciously be utilized. Thus if the sound source itself is held in the hand, it is only with the greatest difficulty that the sound can be localized elsewhere. If the acoustic sensations of distance are not sufficiently strong, the impression will be derived from tactual sensations of the hand. Hence it is essential that all other spatial sensations be suppressed. Of importance also are the various noises that arise from the equipment, in movements of the sound source, and in the manipulations of the experimenter. To avoid these noises a long tube of 8 mm diameter was used to conduct the sounds to the subject, who was blindfolded. The end of such a tube gives a close approximation to a radiator of zero order. In addition, the subject closed both his ears with the fingers while the sound source was being moved and opened them only during the observations. To prevent disturbance from the transients of onset of the loudspeaker, continuous tones were used and were faded slowly on and off. (For the circuit, see Fig. 4-28). With these precautions the perceived distance of pure tones seemed to depend only on the loudness. A suitable variation of loudness could readily make the tone move from 2 to 50 cm. This was not possible for vocal sounds, for example. When the loudness was raised to 100 db above threshold the sound image for high tones seemed to lie immediately in front of the external meatus.

Production of Sensations of Distance. Because continuous tones do not produce sensations of distance, it appears that only impulsive disturbances of the air are effective. Only these give rise to distance cues, and there is no disturbance if a continuous tone is superimposed. The observations showed that of all sound sources the sound of an electric spark in the open air or in a highly damped room was best localized. Such a sound arises because the air is suddenly made to expand by heating. In the upper part of Fig. 8-26 the temporal course of the volume increase ΔV is represented. The middle sketch shows the accompanying velocity of air flow, and the lower sketch shows the pressure changes. For such a click the streaming velocity has an amplitude spectrum extending to the deepest frequencies, whereas for the pressure the deep portion of the frequency spectrum is lacking and there is only a narrow band of frequencies depending on the time course of the volume expansion. Therefore a microphone that is sensitive to velocity will pick up low frequencies in the vicinity of the spark, whereas at a distance these frequencies are absent, for according to Eq. (8-2) only the first derivative of the streaming velocity is effective there. Accordingly, sound sources containing brief bursts of low frequencies seem close at hand, and those containing high frequencies seem farther away.

To study these relations further, a velocity microphone was used to pick up speech sounds from a distance of 25 cm. Then a bandpass filter

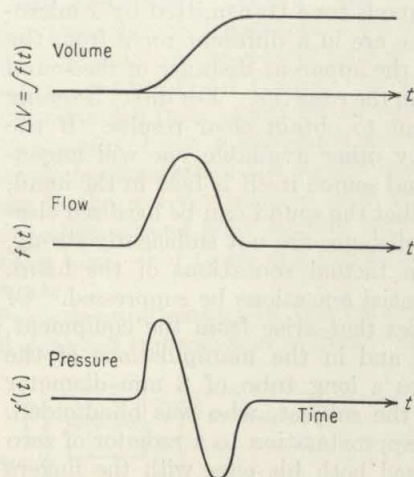


FIG. 8-26. The three curves represent, beginning on the top, the changes in volume, velocity of flow, and pressure of the air as caused by an electric spark.

was introduced into this transmission system. When the low frequencies were transmitted the speaker seemed to be adjacent to the ear, and when the high frequencies were transmitted it seemed to be farther away, as Fig. 8-27 indicates. The distance was indicated by placing the hand at the place where the sound source seemed to be.

The oscillographic records of the click sounds, such as those shown in the upper part of Fig. 8-28, showed large vibrations of low frequencies when the sound source was close to the microphone and, as the lower part of this figure indicates, an absence of low frequencies when the source was far away.

That slow vibrations cause the sound image to be brought close to the ear was shown also by listening to a speaker with the microphone at a great distance and then putting in parallel with the receiver a rectifier shunted by a resistor. If the resistor was large, there was no distortion

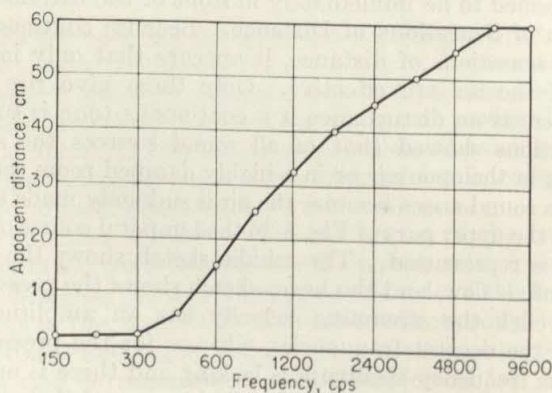


FIG. 8-27. The apparent distance of a speaker as a function of the frequency region of the transmitted band. The points represent the centers of bands one octave wide.

of speech and the speaker seemed far away, provided that the loudness was suitably chosen. If the resistance was made smaller, however, the slow vibrations were increased by the rectifier and the sound image came closer to the ear. It was necessary to avoid any production of difference

tones, for with high tones in particular they are often produced in the loudspeaker, and interfere with the perception of distance.

These results indicate that the following physiological conditions produce the sensations of distance. If there is an excursion of the stapes corresponding to the streaming velocity $f(t)$ as indicated in Fig. 8-26, a traveling wave arises along the basilar membrane. This wave begins at the stapes and is propagated toward the helicotrema, where it subsides. The disturbance produced by a sharp click extends over the entire membrane, so that the timbre always has a certain deep character. The

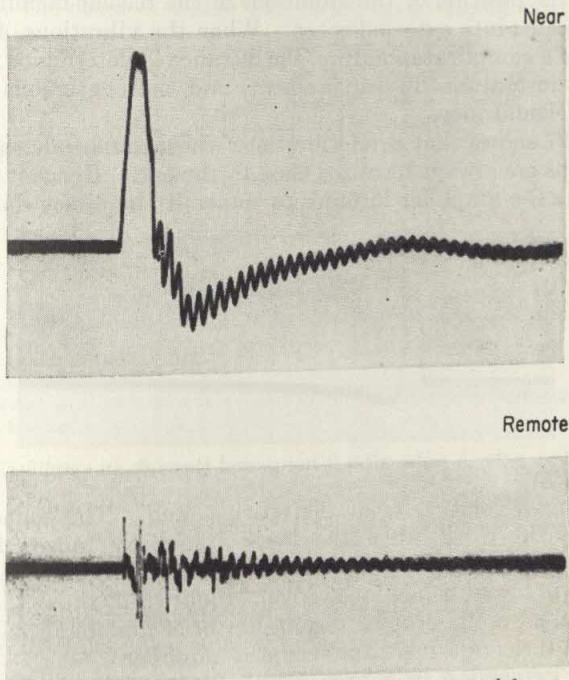


FIG. 8-28. Oscillograms of clicks that seemed near and far away.

shorter the duration of the volume change, the smaller the displacement of the basilar membrane in the region of the helicotrema. This is so because this region of the membrane has a low natural frequency, and a click whose duration is brief relative to the period of vibration produces an amplitude equal to the ballistic deflection. The portions of the basilar membrane in the vicinity of the stapes are tuned to a high frequency, however, and here the displacements can follow the instantaneous values of the stapedial motions. Thus it follows that when the duration of the click is shortened the vibrations of the basilar membrane are concentrated in the region of the stapes.

If the stapes executes vibrations of the form $f'(t)$ as indicated in Fig. 8-26, the vibrations move more and more toward the stapes because the ballistic deflections produced by these vibrations are zero for the deeply

tuned portions of the membrane. Since a distant sound image arises for this type of vibration, it follows that the sound image appears farther away accordingly as the basilar-membrane movement is limited to the region of the stapes. If the portions of the membrane near the helicotrema were also involved in the response to a brief thrust of the stapes, the sound image would approach closely to the ear. Hence the sensations of distance are determined by a change in the location of the basilar-membrane movements for a brief thrust of the stapes. If the vibrations come close to the helicotrema, then the sound image comes close to the ear. Thus the position of the vibrations of the basilar membrane are in a sense projected into external space. When the vibrations of the sound source are of a complicated nature, the distance is determined principally by the first instantaneous displacement, and the continuous vibrations are of little significance.

Figure 8-27 shows that brief vibrations whose amplitude spectrum lies below 450 cps are always localized close to the ear. Hence it is unnecessary to use a d-c amplifier in order to transmit the direct component of

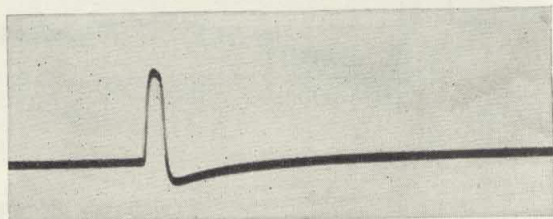


FIG. 8-29. A pulse after it has passed through an amplifier.

the streaming velocity $f(t)$ of the spark sound. The sound image is already brought close when the lower frequency range of the brief unilateral pulse is cut off because it is followed by a prolonged equalization process in the transmission system. Figure 8-29 shows this equalization effect in an oscillographic record of a brief unilateral pulse that has been passed through a resistance-coupled amplifier.

Distance Perception in a Free Sound Field. In order that distance be perceived in a free sound field it is necessary for the ear to act as a velocity receiver. This is the case, as the impedance measurements made by Tröger and Geffcken prove for middle and high tones. In the region of 800 to 2000 cps the impedance of the tympanic membrane often falls to the resistance of the air. In the region above 3000 cps the resonance of the meatus comes into play and contributes further to the reduction of the impedance of the auditory aperture.

In general it is found that in a free sound field any sound source can be localized with certainty and precision up to a distance of about 1 meter. This is hardly to be expected on the basis of physiological conceptions of the sensations of distance. These conceptions indicate that in a free field a source containing high-frequency click sounds ought to be localized at a distance, and one containing low-frequency sounds ought to be localized close by.

The circuit of Fig. 8-30 was used to investigate these points. A rotating switch S was used to connect an oscillatory circuit periodically with a battery and with a short circuit. The resulting pulses of damped waves were led through an amplifier tube with a negative grid bias, which permitted only the first wave of the oscillation to pass through. Thus the loudspeaker was acted upon by a brief current pulse, whose duration could be varied by changing the time constant of the circuit. Switch U served to adjust the damping of the oscillatory circuit and permitted a comparison of the two oscillatory circuits, one of which was held at 300 cps and the other of which was varied up to 12,000 cps.

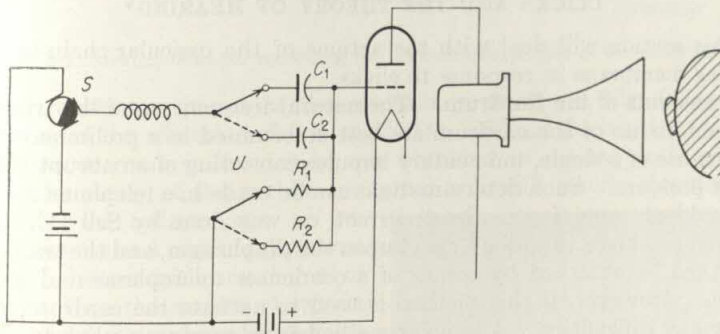


FIG. 8-30. Circuit used to study the effects of the frequency spectrum upon apparent distance in a free field.

If these sounds were listened to under the proper conditions it was possible to obtain displacements of the sound image over a range of 5 to 100 cm. The conditions were as follows: uniaural listening with a loudspeaker of proper size, a sound field as nearly spherical as possible, and a loudness of a comfortable and steady value. To ensure a spherical wave it was necessary that the cone of the loudspeaker be very small, or that it be located behind a small opening in the wall.

If speech sounds that had been passed through a filter were conducted to the loudspeaker, then changes in the passbands led to corresponding alterations in the perceived distance. These results show that for a correct estimation of the distance of a sound source it is necessary to have a certain amount of knowledge about its timbre. If this knowledge is absent, the listener can make a confident judgment of the distance, but this judgment will not be in agreement with the actual distance.

CHAPTER 9

PROBLEMS OF DISTORTION

CLICKS AND THE THEORY OF HEARING*

This section will deal with the actions of the ossicular chain and the basilar membrane in response to clicks.

Transients of the Eardrum. The natural frequency and the transient characteristics of the eardrum are best determined in a preliminary way by the use of a single, momentary impulse consisting of an abrupt change of air pressure. Such determinations can be made in a telephone receiver by suddenly applying a direct current, as was done by Sell (1). This current produces a sudden impact upon the diaphragm, and the transients can then be observed by means of a condenser microphone and oscillograph. However, if this method is used to actuate the eardrum, there are many difficulties. A simpler method is to produce a click from the Eustachian tube in the act of swallowing. This click arises because a movement of the pharynx produces a contraction of the fibers of the tensor-veli-palatini muscle running to the membranous wall of the Eustachian tube. When this muscle pulls in the direction of the pharynx it expands a portion of the tube and thereby produces a change of volume of the middle ear. The tube walls are normally in a collapsed condition and stick together on account of the moistness of the mucous surfaces. When the muscle exerts a certain tension the walls separate and suddenly come to the end of their expansion when they meet the bony enclosure.

After several days of practice many persons are able to produce this click voluntarily and to repeat it in a rapid series without the necessity of swallowing. Though it occurs in both ears, it is usually a little earlier in one. The production of the click in this way does not ordinarily lead to an opening of the tube, as can be proved by the fact that a soft humming sound is unchanged in loudness. When the tube is open, the pressure changes pass directly from the mouth to the middle ear and there produce a strong rumbling sound.

The transient responses of the eardrum were observed by a second person by means of a listening tube or were recorded with a condenser microphone, as Fig. 9-1 shows. To avoid resonance in the cavity between the eardrum and the microphone, the sound was conducted from the eardrum to the microphone through a tube 1.5 meters long and 0.7 cm in inside diameter. With this length of tube the transients had run their course before a reflected wave occurred. Because unexpectedly

* Article 15 as listed in the Author's Bibliography. Published in 1933.

large sound pressures could arise, which might damage the oscillograph, the output transformer of the amplifier was bridged with a glow lamp. This lamp limited the amplitude of the oscillograph string, because an excessive voltage caused it to discharge and short-circuit the transformer.

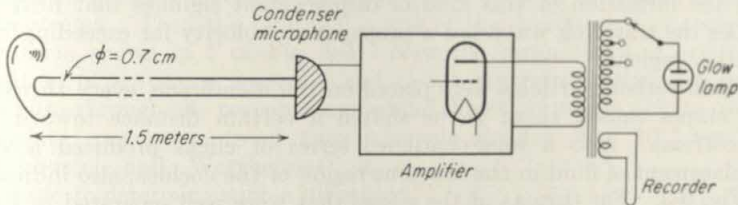


FIG. 9-1. Arrangement for recording the transient responses of the eardrum.

The transient response of the eardrum is shown in Fig. 9-2. The frequency of the vibrations fell from 1500 to 1200 cps during their decay. A similar decrease in frequency was obtained in all the tests. This natural frequency of the middle ear agrees well with results obtained by Frank on the cadaver ear. If we regard the ear as a whole as approximating a system with one degree of freedom, then the results shown in Fig. 9-2 represent an amplitude ratio of two successive waves between 3.0 and 4.0. Therefore the logarithmic decrement ϑ lies between 1.1 and 1.4. Other results show a maximum decrement up to 1.8.

The first half-period of the transients was considerably distorted because the Eustachian tube required a certain time to expand, and so the time of the applied pulse was long relative to the period of vibration. Also this first half-period changed after several repetitions of the click, though the succeeding vibrations were unaltered.

Transients of the Basilar Membrane. The vibrations displayed by the basilar membrane were investigated with the cochlear model described elsewhere (page 405). It was seen with stroboscopic illumination that before any vibrations occurred there was a momentary displacement of the stapes and adjacent to the stapes a synchronous pistonlike movement of the fluid. The portion of basilar membrane up to the place where an eddy arises for 1000 cps underwent a momentary displacement, while the region near the helicotrema remained at rest. This condition is shown in Fig. 9-3 by the solid curve. A little later the portion near the

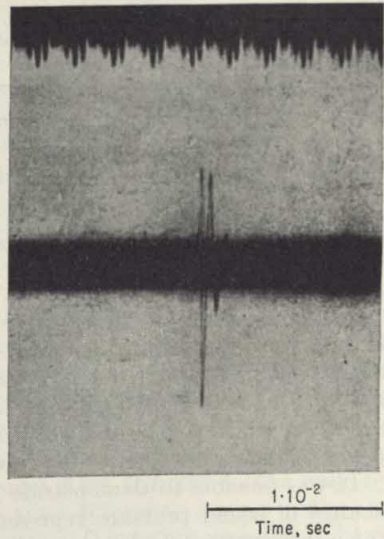


FIG. 9-2. Transient vibrations of the eardrum. At the top is a time trace.

stapes returned aperiodically to its resting position, while a flat traveling wave appeared at the other end, as shown by the broken curve. This wave subsided at the helicotrema in about $\frac{1}{20}$ sec. The displacement up to the 1000-cps area resembles that of a telephone-receiver diaphragm, and the formation of this kind of displacement signifies that near the stapes the traveling wave has a propagation velocity far exceeding that in other regions.

When carbon particles were placed on the membrane, every thrust of the stapes caused them to be shifted a certain distance toward the helicotrema. Also a long-continued series of clicks produced a slow displacement of fluid in the low-tone region of the cochlea, also indicated in Fig. 9-3. For thrusts of the stapes that were well separated in time, the resulting fluid displacements were finally equalized at the helicotrema, and as a result of rectification processes two pairs of eddies arose. In the actual ear these eddies are relatively small on account of the particular form of the helicotrema.

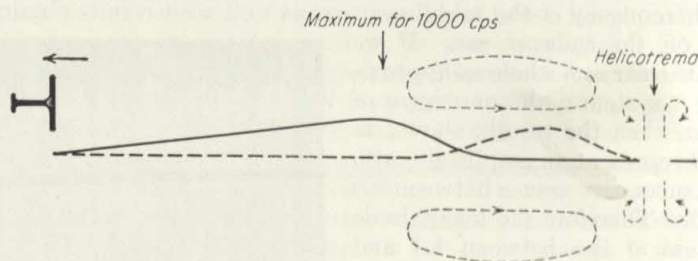


FIG. 9-3. Traveling waves on the basilar membrane produced by a sudden displacement of the stapes to the left.

If the transients of the eardrum shown in Fig. 9-2 were conducted to the stapes so that vibrations were applied to the membrane of the model corresponding to the momentary pressure change in the auditory meatus, the first half of the membrane followed the vibrations of the stapes exactly. In the region of the helicotrema, however, there were two wave peaks of the damped traveling waves.

It was possible to demonstrate in the human ear also that a sudden change of sound pressure representing a rapidly declining transient of the eardrum produced a traveling wave along the basilar membrane. This wave at first progressed with great speed from the stapes toward the helicotrema but later moved more slowly.

Consider the temporal course of the transients of the stapes as shown in Fig. 9-4*a*. They produce a temporal pattern of excitation of the nerve endings in the region of the stapes as shown in *b* of this figure, when account is taken of the latencies and aftereffects in the nerve fibers. The temporal course of excitation of the whole basilar membrane, however, is extended by the final velocity attained by the traveling waves, as shown in *c*. Because a weak click sounds high in pitch, it appears that the stimulation is mainly in the high-tone region of the basilar

membrane close to the stapes and not in the low-frequency regions where the curve falls below threshold. On the other hand, a stronger click has a dull sound because the opposite relations hold, as Fig. 9-4c shows.

If on the loud click a continuous low-frequency tone is superimposed, there is a masking of the stimulation by the click in the region near the helicotrema. Then the temporal course of the excitation once more has the form shown in *b* of Fig. 9-4. Now the mean times of excitation (centers of gravity of curves *b* and *c*) can represent a time difference. Because through the perception of sound direction we are able to obtain accurate measurements of time intervals smaller than 10^{-4} sec (see Hornbostel and Wertheimer) it is possible to determine such a difference.

For this purpose clicks were produced by suddenly applying a direct current to a condenser receiver. This sound was introduced into one ear at a loudness equal to that of a 1000-cps tone 60 db above threshold. The same stimulation in the other ear gave a sound that was perceived in the mid-line of the head. A tone was then superimposed upon the sound in one ear at a loudness equal to that of the click. If this tone was low in frequency, the click became high in pitch; and if the tone was high in frequency, it became low in pitch, while its loudness was generally decreased. If the undisturbed click was weakened to the point where it was equal to the click that was masked by the tone, then

when both clicks were presented together it was necessary to delay the masked one by the amount shown in Fig. 9-5 in order to keep the sound image in the mid-line. At 100 cps the time difference was so large that for most subjects a simultaneous presentation of the two clicks produced two separate images. These two images were reduced to one only by compensating in some degree for the time difference arising in the ear by introducing an external time difference. It was not essential to have an exact equation of the loudness of the clicks on the two sides, for in most subjects the judgment of sound direction was not affected by small differences of intensity. This fact was established in preliminary experiments (page 298).

It has been shown that a direct current applied to a thermophone produces almost as rapid a rise of sound pressure as is produced in a condenser type of receiver. There is at most a displacement of the sound image of 1 cm if one side of the head of the condenser receiver is replaced by a thermophone. Therefore a thermophone was used for control measurements.

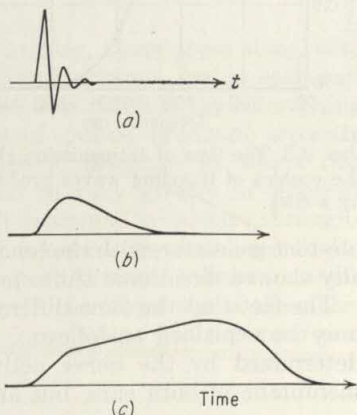


FIG. 9-4. Curve (a) is a transient of the stapes, curve (b) is its effect on the nerve endings near the stapes, and curve (c) is the whole course of excitation over the basilar membrane.

As may be seen in Fig. 9-5, frequencies above 800 cps no longer produced a directional shift when used as masking tones in the manner described, though here we should expect a displacement of the image in the contrary direction because a masked click ought to produce a delayed excitation.

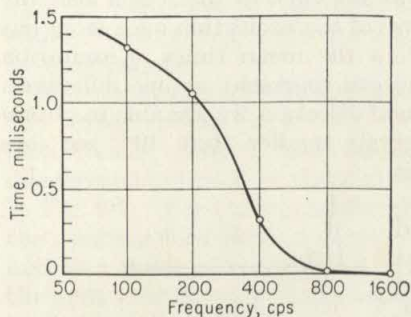


FIG. 9-5. The time of transmission along the cochlea of traveling waves produced by a click.

The reason may be that it is not possible for a single tone to cover a large area of the basilar membrane, as in fact is indicated by the masking curves obtained by Wegel and Lane. Also the basilar membrane is much narrower and stiffer in the vicinity of the stapes, so that here the propagation velocity of the traveling wave is much greater than near the helicotrema. Therefore the same degree of masking can give rise to only a small time difference. Experiments with a multi-

ple-tone generator, with the tones below 800 cps filtered out, only occasionally showed directional shifts toward the side of the undisturbed click.

The fact that the time differences are small even with low frequencies may be explained as follows. Perhaps the direction of a sound is not determined by the nerve activity of the entire length of the basilar membrane of both ears, but arises from the interaction of very narrow

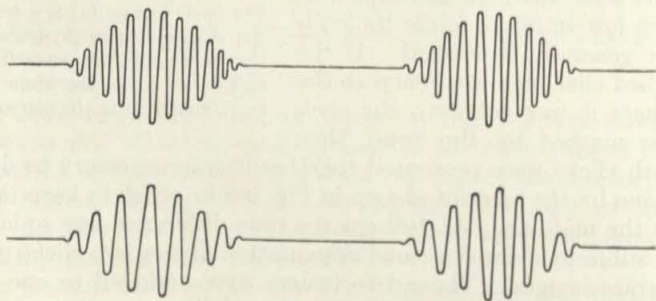


FIG. 9-6. Tone pulses used to stimulate the two ears.

regions of the two membranes. Then the time difference observed will be limited by the time required for the traveling waves to pass over these two corresponding regions and not by the much longer time required to traverse the whole membrane.

The following experiment supports the view that only limited areas of the basilar membrane are operating in this way. A tone pulse of the form represented in Fig. 9-6 was produced by altering the grid bias of an amplifier tube (Fig. 4-28). When this change of bias was caused by an alternating current of 5 to 10 cps, the amplitude changes in the tone produced by the amplifier were so slow that the tone pulses were free

of noise. Then the same regions of the basilar membrane were stimulated as when a continuous tone of the same frequency was used. On the other hand, the amplitude change was rapid enough that when such a series of pulses was heard simultaneously by both ears there was a directional effect. This effect depended simply on the temporal course of the amplitude change and was little affected by a phase shift in the tone. If the temporal course of the amplitude was the same in the two ears, and if the loudness of the series of pulses was equal also, the sound image was perceived in the mid-line of the head. Also, its position did not change when the frequency of the pulses produced in the two ears was made somewhat different. The sound image then represented a pulsating complex of tones.

If the frequency difference was made greater, there arose along with the image in the mid-line a pair of additional images, one in each ear. Then when a certain frequency difference was reached the intervening image disappeared, and the two series of pulses produced separate sensations in the two ears. The frequency difference at which this separation of images appeared was found to vary greatly in different individuals, though for any one person it remained consistent throughout a series of observations. Table 9-1 shows the upper and lower limits at which a tone pulse of 1000 cps 60 db above threshold showed a complete separation of the images. A change in the frequency of the alternating current applied to the grid from 5 to 20 cps had no important effect upon these limits.

TABLE 9-1

	Subject A	Subject B	Subject C
Upper limit.....	2900	3020	2100
Lower limit.....	550	330	240

The following experiment was carried out to find how long it takes for the transient vibrations of the eardrum to decline to the point at which there is no further influence on the perception of a click. As Fig. 9-7 indicates, in one situation, *a*, there was first a sudden increase in the sound pressure, it was held for a time Δt at this increased value, and then it was restored to its initial level. In a second situation, *b*, the sound pressure was raised suddenly, held for a time Δt , and then raised further by the same amount as in the preceding step and held at this doubled level for a long time. The smallest time interval Δt between the first and second changes was determined for which these two series could not be distinguished from each other. In this test the two series were presented about once per second. To avoid any disturbance on switching off the doubled pressure, a condenser was shunted across the source to give a gradual decline of the current so that it became inaudible.

If the clicks had a level 40 db above threshold, they seemed louder when the sound pressure was doubled, as long as the interval Δt was small.

But when this interval exceeded 4×10^{-4} sec, there was complete equality of loudness in the two situations. This result agrees with the work of Steudel. For intervals up to 3×10^{-3} sec the timbre was noticeably duller for the doubling situation, and for a further increase in the interval the timbre became brighter. For an interval of 5×10^{-3} sec the timbre was indistinguishable in the two situations.

These times are sufficient to allow the two traveling waves on the basilar membrane to coexist without any influence on each other. Yet the duration of a click sensation is noticeably greater. If a change in sound pressure equal in loudness to the above series of clicks was masked by a strong tone of 600 cps, the change in sound pressure had to precede the momentary masking tone by about 1×10^{-2} sec if the click was to be perceived. Yet at least 0.2 sec was necessary to prevent any effect

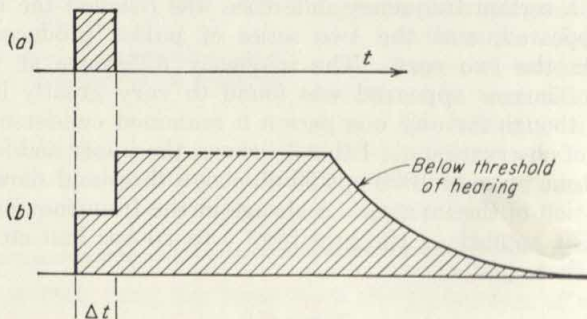


FIG. 9-7. Two forms of sound-pressure changes presented to the ear.

on the timbre and loudness of the click by the large burst of loudness of the masking tone (Steudel).

If the sound pressure in the meatus is not raised instantaneously to its final value but, for example, is raised in proportion to the time, this pressure change produces a displacement of the stapes that is likewise linear with time. This is true because the transients of onset are greatly reduced by the heavy damping of the middle ear.* If observations are made in the model of the ear of a stapes displacement that is proportional to the time, the basilar membrane in the region of the stapes bulges out at the first instant that the stapes displacement occurs. It then maintains this position until the stapes displacement disappears. Because of frictional forces, the continuous flow of fluid through the helicotrema toward the round window produces a pressure gradient on both sides of the basilar membrane. Hence it is clear why the click produced by a slow rise or fall of pressure is changed but little in loudness if the pressure change is stopped after a short time instead of being maintained (Steudel).

* If the transients produced by an instantaneous pressure change are known, the onset processes can be calculated by Carson's method.

Finally, Fig. 9-8 shows for two subjects the effects of various frequencies used in the masking of a click. The loudness of a click produced by a momentary change of pressure was made equal to that of a tone of 1000 cps at a level 40 db above threshold. The loudnesses of the various tones that just masked the click were obtained also by comparing them with

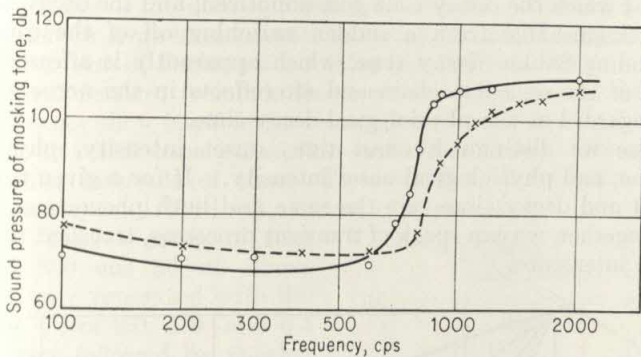


FIG. 9-8. The masking of a click by continuous tones of various frequencies. Results are shown for two subjects. Sound pressure is represented in decibels above 3.16×10^{-4} dynes per sq cm.

a tone pulse of 1000 cps. These loudnesses are expressed in decibels on the ordinate.

AUDIBILITY OF TRANSIENTS*

The sudden introduction of a sinusoidal tone into a room produces transients of onset, and the cessation of the tone produces transients of decay. The effects are greatly distorted by interference phenomena. By warbling the tones it is possible to avoid the production of nodes at particular places in the room and to obtain reasonably uniform transients. Yet such tones are unsuitable for observations of audibility, for their high degree of roughness makes it difficult to measure temporary variations of loudness.

Accordingly, it seemed best to investigate first the simplest form of transients, namely, those in a tone pulse presented by an earphone. In this way the physiological aspects of the transients may be related to the appropriate physical dimensions.

The procedure and equipment used for this purpose are described in Chap. 4, page 58 and Figs. 4-27 and 4-28.

Definitions. To avoid misunderstandings, the following terms will be used. Along with the decay time of Sabine, which is called the reverberation time and is given by the time required for the sound pressure to fall 60 db, we also use the actual decay time, as Schuster and Waetzmann did, as the time that the tone requires to fall from its original value to the auditory threshold.

* Article 14 as listed in the Author's Bibliography. Published in 1933.

For every physical decay time there is a certain sensation of decay that depends not only on the time but also on the intensity of the tone, its frequency, etc. We shall speak of the decay intensity of this tone, which bears the same relation to the decay time as loudness bears to sound pressure. As the decay time of a tone is reduced, a value is finally reached at which the decay time goes unnoticed, and the decay processes are indistinguishable from a sudden switching off of the tone. The corresponding Sabine decay time, which apparently is affected by the mobility of the ossicular chain and aftereffects in the nerve elements, will be regarded as the physiological decay time.

Likewise we distinguish onset time, onset intensity, physiological onset time, and physiological onset intensity. If for a given tone pulse the onset and decay times are the same and both phenomena are considered together, we can speak of transient processes, transient times, and transient intensities.

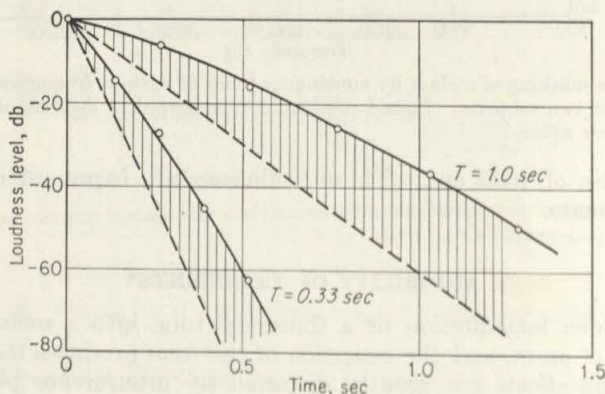


FIG. 9-9. Lag in the decay of loudness of a tone. The broken lines represent the actual decay of sound pressure.

Decay Processes. In general, the decay processes exhibit four features of interest. We can consider first of all the actual decay time, much as Sabine did in his reverberation-time method. In this case we simply indicate the time at the beginning of the decay process and the moment when the threshold is reached. Then the time interval between these two is related to the loudness, the difference limen, and so on in the same way as any time interval defined by two time marks.

Secondly we can consider the loudness attained at any given instant. Just as the loudness of a tone does not follow exactly a sudden increase in intensity (see page 358) but requires about 0.2 sec to reach its final value, so also in this situation the loudness lags behind the decay processes. If a tone is presented at constant amplitude for 0.3 sec and is then broken off after it has been allowed to decay for a certain period of time, its loudness at the moment of interruption is greater than that of a tone pulse presented to the other ear at the sound pressure existing at this moment of interruption. Figure 9-9 shows, for an 800-cps tone 80 db

above threshold and decay times $T = 1.0$ and $T = 0.33$ sec, how much more slowly the loudness declines in time than it would if it corresponded to the sound pressure of a continuous tone. Here the loudness is measured in decibels above the threshold of the tone pulse.

A further feature is the rapidity of the decline of loudness, especially at the beginning of the decay process. The decline of loudness is somewhat greater for large loudnesses than for small ones, in agreement with the modified form of Fechner's law (*cf.* pages 245 and 370).

The fourth feature, which is the most important one in listening to music, does not show itself in the decay processes as such, but rather in the extent to which tone pulses fuse with one another when separated by particular intervals of time. To determine the relation between decay intensity and loudness, curves of equal decay intensity were

obtained. Thus a series of tone pulses of 800 cps 80 db above threshold were presented with decay times T_0 of 2.0, 1.0, and 0.5 sec and were followed by another series of pulses whose decay times T were varied until the decay intensities of the two successive series seemed the same in spite of their different loudnesses. When various loudnesses were used for the second series, the results were as shown in Fig. 9-10. The measurements were carried out by a bracketing method, with T made first longer and then shorter so that there was a clear difference between the decay time of T and T_0 . The final value was then obtained

by bisection. The results were not significantly affected if the interval between pulses was altered within a range of 0.3 to 3 sec, and the decay processes did not always reach threshold. Also it did not matter whether the two tone series that were being compared were led successively to one ear or successively to the two ears. The threshold was always measured with a pulse lasting 0.3 sec.

The broken curves represent actual decay times that are equal. As is evident, these curves do not depart markedly from the observations. As the loudness decreases the decay intensity falls off less rapidly than the actual decay time. If the decay time is in the region of 0.5 to 2.0 sec and the interval between individual tone pulses is greater than 0.3 sec, then the decay intensity

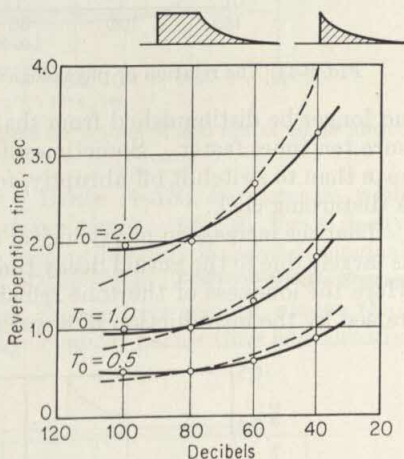


FIG. 9-10. Curves of equal decay, for 800 cps.

$$D = Kt_{w}^{0.8} \quad (9-1)$$

when t_w is the actual decay time.

If the interval between individual pulses becomes less than 0.3 sec, the exponent in Eq. (9-1) declines rapidly in magnitude and finally becomes zero, except when fatigue enters for extreme loudnesses.

As the decay time is made smaller and smaller, the physiological decay time is approached. Its magnitude as a function of the loudness is shown in Fig. 9-11. Thus it is established that the decay time of a declining tone is gradually reduced to the point where the decay process can

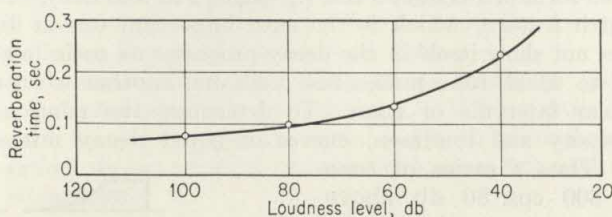


Fig. 9-11. The relation of physiological decay time to loudness, for 800 cps.

no longer be distinguished from that of a tone that is falling off in pressure ten times faster. Sometimes it is better to reduce a tone at a rapid rate than to switch it off abruptly, for the sudden switching may produce a disturbing click.

That the increase in physiological decay time with diminishing loudness is largely due to the actual decay time is shown by the results of Fig. 9-12. Here the loudness of the tone remained constant, and the threshold was raised by the introduction of a warble.

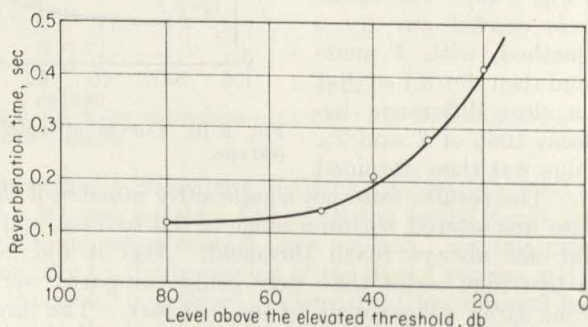


Fig. 9-12. The physiological decay time when the threshold is raised by means of a noise. The tone was 800 cps at 80 db above threshold.

For a determination of the difference limen for the decay time an automatic switch was used to present a series of tone pulses of a duration of 0.3 sec, each of which was followed by a similar decay process. This series was then compared with a second series of equal loudness, whose decay times were lengthened or shortened until a clear difference was perceived. The percentage of change in the damping resistance R_2 in the resonant circuit of Fig. 4-27 that produced a just-perceptible difference is shown in Fig. 9-13 for a tone of 800 cps 60 db above threshold.

This percentage of change in resistance is approximately equal to the change in decay time $\Delta T/T$ when the changes are small.

In the most important range of decay times between 2.0 and 0.5 sec the difference limen was about 10 per cent, both for shortening and lengthening of the decay time. If the decay time became smaller than 0.3 sec, however, it approached the physiological decay time, and a further

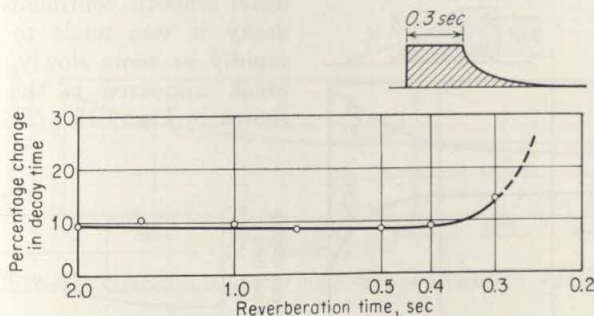


FIG. 9-13. The difference limen for decay time for a tone of 800 cps at 60 db above threshold.

shortening was no longer noticeable. Hence $+\Delta R_2/R_2$ increases with great suddenness. A reduction of decay time $-\Delta R_2/R_2$ for a decay time that was short to begin with was perceptible only if the physiological decay time was exceeded. In the loudness range of 80 to 40 db above threshold the difference limen did not change appreciably, except that for the smaller loudness levels the physiological decay time had already

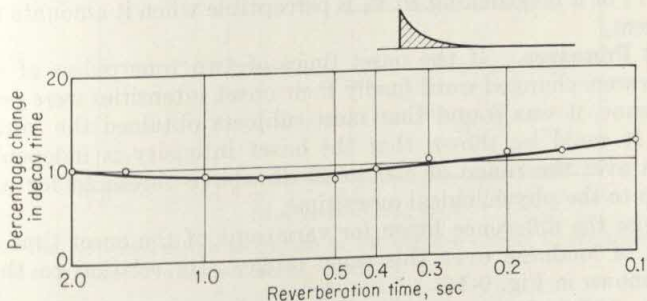


FIG. 9-14. The difference limen for decay when only a brief decay transient is presented.

been reached for the larger values of decay time T , and therefore the curve rose somewhat sooner. These observations were disturbed by the fact that in the beginning the difference limen fell off continually with practice, partly because of the fact that the switching processes had a distracting effect.

If in place of the tone pulses of 0.3 sec duration with their subsequent decay a momentary, abrupt decay process was used, the difference limen had the values shown in Fig. 9-14. For these brief times the dif-

ference limen did not increase, because only a variation in the timbre of the click was associated with the change of decay time. The values did not change when the interval between the pulses was altered.

There is a question as to what extent variations in the form of the decay processes can be perceived. A tone was made to decay to a level

of 40 db, and then instead of the usual smooth continuation of the decay it was made to fall more rapidly or more slowly, so that a break appeared in the curve as shown in Fig. 9-15. The ordinate

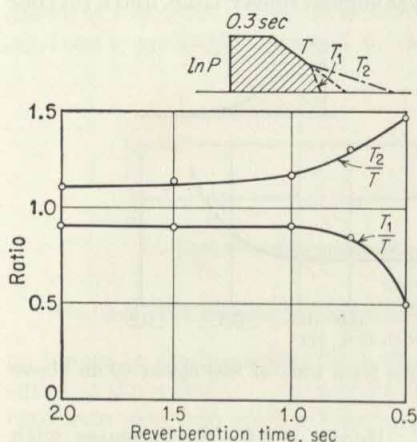


FIG. 9-15. Effects of variations in the form of the decay curve for 800 cps at 80 db above threshold.

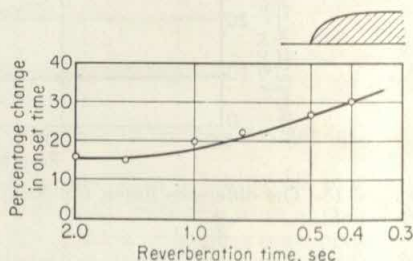


FIG. 9-16. The difference limen for onset time for 800 cps at 60 db above threshold.

of this figure represents the ratio of the decay times in the second and first halves of the course of decay. For the longer decay times a reduction to T_1 or a lengthening to T_2 is perceptible when it amounts to 10 or 20 per cent.

Onset Processes. If the onset times of two tone pulses of unequal loudness were changed until finally their onset intensities were perceived as the same, it was found that most subjects obtained the same onset times. It could be shown that the onset intensity is independent of loudness over the range of 100 to 40 db above threshold for all onset times up to the physiological onset time.

Likewise the difference limen for variations of the onset time is independent of loudness over this same range. Its relation to the onset time is shown in Fig. 9-16.

In Fig. 9-17 is shown the relation of the difference limen to frequency for a level of 60 db above threshold and an onset time of 1.5 sec. If the frequency was raised, beginning with the lowest tones, the initial impression of vibration and roughness passed over into a completely smooth sensation of tone. It was easier to follow the onset and decay processes in this smooth sensation than in one with considerable roughness, and therefore the difference limen was smaller for high than for low tones. If the high tones were deliberately made rough by the introduction of beats, the difference limen was greatly increased.

The physiological onset time was determined by reducing the onset time of the resonant circuit of Fig. 4-27 until no difference could be found

between it and an onset time that was one-tenth as large. A time T of 0.7 sec was obtained for the range 100 to 40 db above threshold, independently of intensity. If the physiological onset time was obtained by a comparison with a tone that was switched on suddenly, the values were usually larger because this switching produced a click that disturbed the observation.

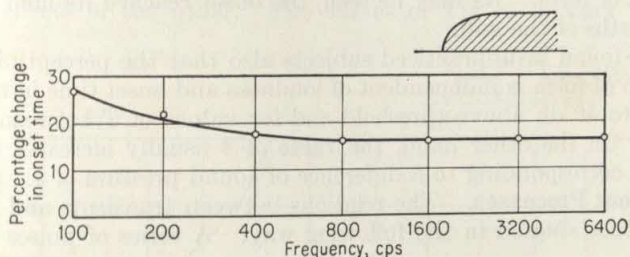


FIG. 9-17. The difference limen for onset time as a function of frequency.

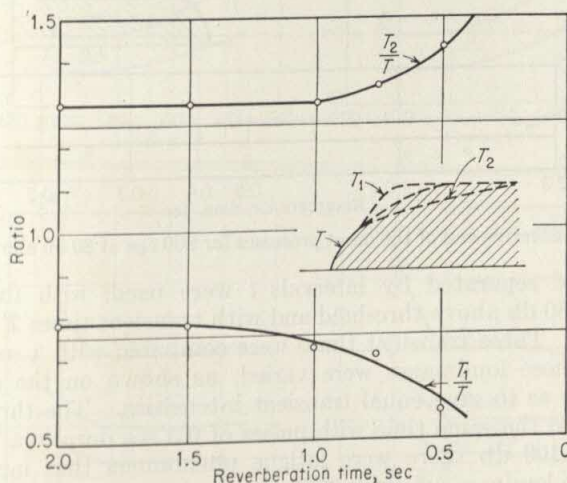


FIG. 9-18. The just-perceptible alteration in the regular course of the onset process for 800 cps at 80 db above threshold.

An indication of the just-perceptible distortion of the onset processes was obtained by lengthening or shortening the onset rate after it had reached its usual halfway point and comparing its effects with those of an onset process that took its usual course. The results are shown in Fig. 9-18.

The perceived length of the onset processes was studied in the following way. At a certain time t , measured from the beginning of the onset process, interrupter U_1 was opened so that condenser C was no longer charged, and therefore the sound intensity remained constant. The onset process that was cut off in this way was compared with a normal one and changed by varying resistance R until a difference was just

perceptible. In order that this change in the form of the onset process would not be recognized as a reduction of loudness, the potentiometer in front of the phone was always adjusted first to give equal loudness for the end tone, and only then was a comparison made of the form of onset. Figure 9-19 shows for a practiced subject the extent to which the sound intensity could fall short of the end value without any perceptible variation of form. As may be seen, the onset reached its final value at three-fourths of the end.

It was found in unpracticed subjects also that the perceptibility of a distortion of form is independent of loudness and onset time in the range from 80 to 40 db above threshold and for values of T between 2.0 and 0.2 sec. On the other hand, the value of δ usually increases up to 42 per cent, corresponding to a difference of sound pressure of 4.7 db.

Transient Processes. The relations between transients and loudness were further studied in the following way. A series of pulses of equal

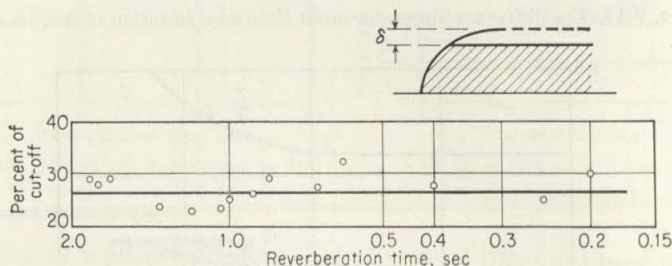


FIG. 9-19. The effective end of the onset processes for 800 cps at 80 db above threshold.

duration and separated by intervals t were used, with the loudness constant at 80 db above threshold and with transient times T of 2.0, 1.0, and 0.5 sec. These transient times were compared with a second series of pulses whose loudnesses were varied, as shown on the abscissa of Fig. 9-20, so as to give equal transient intensities. The threshold was determined at the same time with pulses of 0.3 sec duration. For loudnesses over 100 db there were fatigue phenomena that increased the variations in loudness (*cf.* page 357) and made it necessary to use larger transient times than would have been necessary otherwise.

As the interval t was reduced, there was a reduction of the limits within which the loudness varied, because of the great overlapping of the transients. Moreover, because of the long latency of the nerve elements of about 0.2 sec, the loudness only partly followed the rapid changes in sound intensity, and the loudness variations approached the difference limen for amplitude. The transient intensities, as shown by the two lower graphs of Fig. 9-20, are independent of loudness, because the difference limen also is independent of loudness in the range of 80 to 40 db above threshold. For greater loudness the phenomena of fatigue become important, and the curve undergoes a sudden rise. Because of this great effect of fatigue with its large individual differences, the various series of pulses were presented to the ear for the least possible time.

In order to study the changes of transient intensity in relation to the tempo of a musical passage, a series was made up consisting of bursts of pulses of 0.3 sec duration and transient times T alternating with silent periods of duration t . This series was compared with another faster or slower series whose transient time T was varied to obtain equal transient intensities. The first series thus was used as a measure of the overlapping effects in the other. The curves of Fig. 9-21 show that the

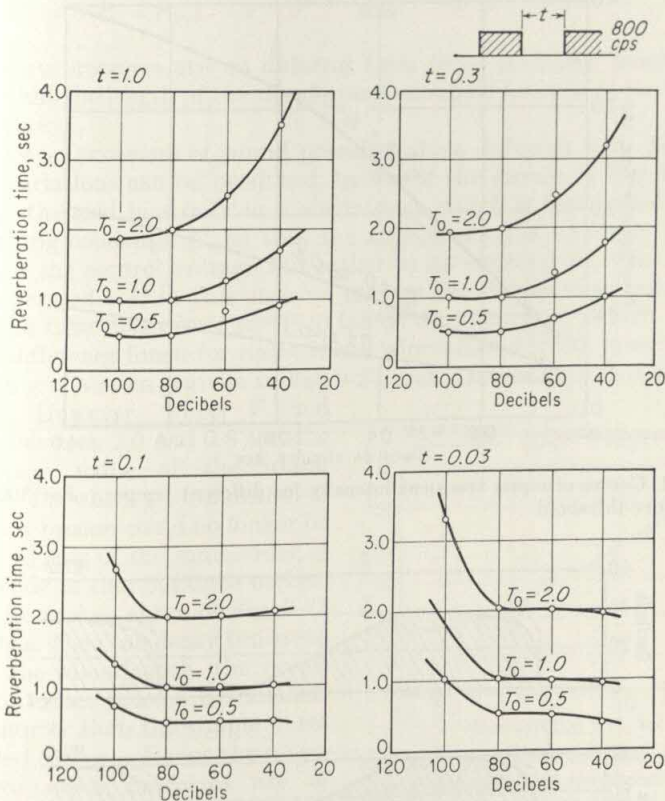


FIG. 9-20. Curves of equal transient intensity.

transient time T rises more slowly than the length of the silent periods t . This fact signifies that rapid changes of loudness are more impressive than slow ones.

If the upper portions of Fig. 9-20 are compared with Fig. 9-10, it is seen that there is no important difference between the loudness relations and the decay intensities of the transients, and hence Eq. (9-1) serves to express the relation to the actual decay times for the transient intensities also.

This relation means that in comparison with the decay intensity the onset intensity has nothing of importance to contribute to the transient

intensity. If this were not the case, then when the onset processes were combined with the decay processes there would be a change in the loudness relations of the transient intensities, as the onset intensity is independent of loudness.

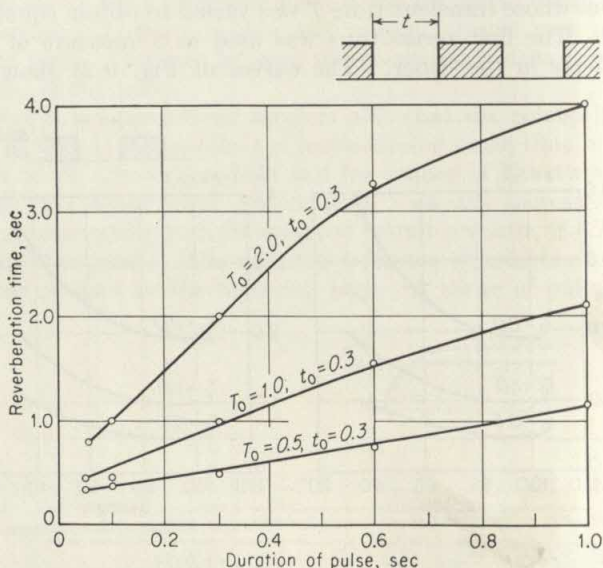


FIG. 9-21. Curves of equal transient intensity for different tempos. For 800 cps at 80 db above threshold.

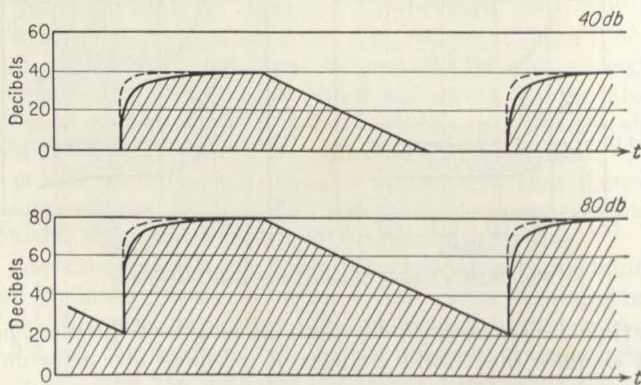


FIG. 9-22. Effect of loudness upon transient intensity.

That the decay process practically determines the transient intensity can be expected from the schematic drawings of Fig. 9-22. Here it is assumed that the loudness, in accordance with Fechner's law, is practically equal to the number of decibels above threshold. It is obvious that a given series of pulses will undergo more overlapping of transients when the loudness is great than when it is small.

Transients in Room Acoustics. When a sound is suddenly switched on and off there are variations in the density of sound energy in a room, assuming a high degree of intermixture of the sound waves, according to the formula $E = E_0(1 - e^{-at})$ for the onset and $E = E_0e^{-at}$ for the decay. Here a represents the damping of the room and t the time.

The important dimension for hearing is not sound energy but sound pressure, for the ear is a pressure receiver. Hence

$$P = P_0(1 - e^{-at})^{1/2} \quad \text{and} \quad P = P_0e^{-at/2}$$

The decay processes are no different from those formerly investigated, except that the length of the decay time is doubled because of the square-root relation.

The onset processes of sound pressure take a different form, however. These variations can be produced, by use of the circuit of Fig. 4-28, by varying the grid bias only in a single stage which is terminated by the discharging condenser C , so that the amplification is no longer proportional to the control voltage but rather to its square root, when switch U_3 is operated. If in this case we take as the Sabine onset and decay times the time taken for $P_0e^{-at/2}$ to fall 60 db, then $T = 13.8RC$.

The difference limen for onset times as obtained for the reverberation transients of a room is given in Fig. 9-23, and is larger than that obtained earlier. However, when T had values between 2.0 and 0.8 sec, the percentage value of the sound pressure for which a termination of the onset process could no longer be perceived was of the same order of magnitude as that obtained earlier.

As the broken curve of Fig. 9-22 indicates, when the decay processes are of the same length, the reverberation onset process is considerably shorter than the simple onset observed earlier. Hence the reverberative onset processes are of much less importance than the decay processes. This is why the curves of equal decay intensity for reverberative decay processes agree with the curves of Fig. 9-20.

There is further evidence that the onset processes are of limited physiological significance in connection with musical transients. Thus in listening to a phonograph record of a musical passage made in a reverberant room, all subjects experience an increase in intensity when the reverberation is increased. Also singers often report that they are not expected to produce their full intensity of voice in a reverberant room.

The loudness relations of transients, as shown in Fig. 9-20, hold only for long intervals between the individual pulses. Hence it follows that in

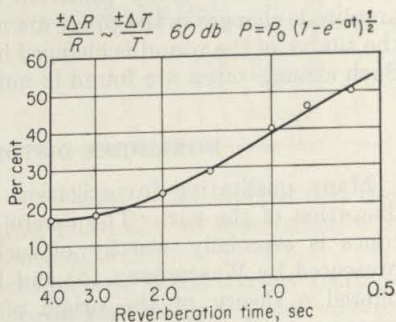


FIG. 9-23. The difference limen for onset time as obtained for reverberation transients corresponding to those of a room.

musical passages the rapid trills are of less importance in producing a fusion of the components than the places in which long decay transients are present.

Though the onset time does not seem to have much physiological significance, there is great importance to the relation between the sound pressure P of the direct sound field with which the sound onset begins and the terminal value of the sound pressure P_0 which is determined by the reflected field. Benecke came to this same conclusion. It may readily be demonstrated by varying the distance of the subject from the source of sound in a large room. In this situation P_0 remains practically constant, while P varies with the distance. However, this relation does not indicate the extent to which the onset processes are shortened by the momentarily appearing direct sound field. Rather, because the direct field is distinguished from the reflected field both in timbre and in its temporal characteristics, the different loudness relations in the two fields affect the audibility.

A number of opinions are held on the question whether optimal acoustics in a room are afforded by a certain reverberation independently of the room itself, or whether a direct part is played by temporal effects such as the actual reverberation time or the period of the conscious present, or whether several of these phenomena operate together (Lifschitz; Schuster and Waetzmänn; Benecke).

The onset and decay processes of the room, which arise simply as amplitude changes in the tones, are modified if during the onset and decay the timbre of the sound is changed by variations in the overtone content. Such changes often are found in musical instruments.

NONLINEAR DISTORTION IN THE EAR*

Many qualitative investigations have been made of the nonlinear distortion of the ear. The careful study by Stumpf (3) on difference tones is especially worthy of mention. General reviews have been presented by Waetzmänn (5) and E. Meyer (2). Waetzmänn (8) also offered a theory of the origin of difference tones. Apart from the measurements of Wegel and Lane, however, no quantitative results are available on the overtones and difference tones arising in the ear.

Overtones Produced in the Ear. To determine the magnitudes of the overtones arising in the ear the exploring-tone method was used.† As shown in Fig. 9-24, one channel consisting of a generator G_1 , an attenuator b_1 , and a filter led to a dynamic telephone receiver, and produced a fundamental tone, say, of 400 cps. A second channel leading to the same receiver produced a tone that departed slightly from the

* Article 17 as listed in the Author's Bibliography. Published in 1934.

† [On the basis of later experiments, described in Chap. 13, page 577, the writer is now of the opinion that the exploring-tone method does not give any information concerning nonlinearity of the ear. The amplitude of the exploring tone giving best beats is actually determined by a pattern of vibration representing the sum of the fundamental and the exploring tone. See Chap. 13, page 588. The above paper was included here because the measurements of best beats are still of interest.]

frequency of the overtone to be measured. This tone was adjusted in sound pressure so that the beats between it and the overtone were at a maximum. To prevent any interaction of the two sound sources, the channels were connected to the receiver through a bridge network. To determine whether the fundamental tone was sufficiently free of overtones, the receiver was connected to a Quincke interference-tube system, as shown. One loop of this system contained a filter that would not pass the overtone, and both loops contained cotton for acoustic damping. By adjusting the length of one loop (for phase opposition in the two loops) and suitably clamping the rubber tubes (for equality of intensity for the fundamental in the two loops) it was possible to eliminate the fundamental, so that at the listening point on the right only the overtone was heard. The loudness of this overtone was then compared with a tone

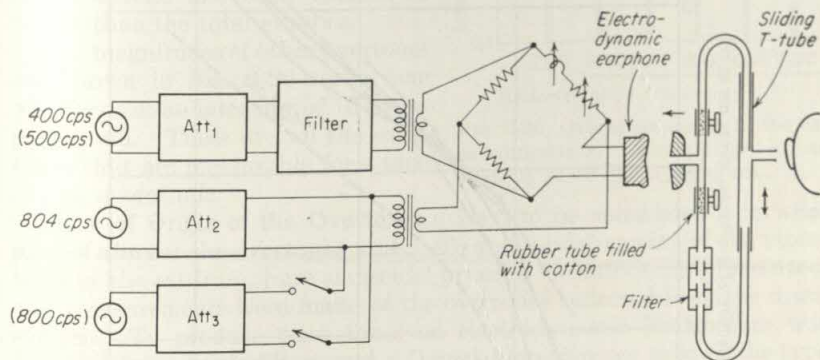


FIG. 9-24. Circuit for the measurement of overtones arising in the ear.

of the same frequency in channel 2. This observation showed that the amplitude of the overtone, even at great intensities of stimulation, was at least 50 db below that of the fundamental.

The small magnitude of the overtones present in the receiver relative to those produced in the ear could be proved also by holding the receiver a little distance from the ear. Then the loudness of the fundamental was reduced, and to obtain maximal beats it was necessary also to reduce the amplitude of the exploring tone. If the overtones in the receiver were stronger than those arising in the ear, the withdrawing of the receiver would not affect the beating with the exploring tone, for the magnitude of the overtones present in the receiver would not be altered.

The best beat frequency was about 4 cps. To prove that for best beats the amplitude of the exploring tone is actually equal to that of the overtone, the following procedure was carried out. With the fundamental canceled out in the manner described, channel 3 of Fig. 9-24 was switched in and the frequency of its generator was made to equal the overtone. Then the attenuator of channel 2 was adjusted for maximal beats. This beating was masked by a strong tone from channel 1, which was adjusted to a frequency a little different from that of the fundamental

so that its overtones did not coincide with the two beating tones. It was found that for most subjects after a little practice the masking tone had no effect upon the adjustment for best beats. When an effect was present, it was necessary to correct the loudness of the masking tone, but this correction never exceeded 8 db in these measurements.

The sound pressure obtained for the second and third harmonics of a tone of 800 cps presented at various sound intensities, as shown on the

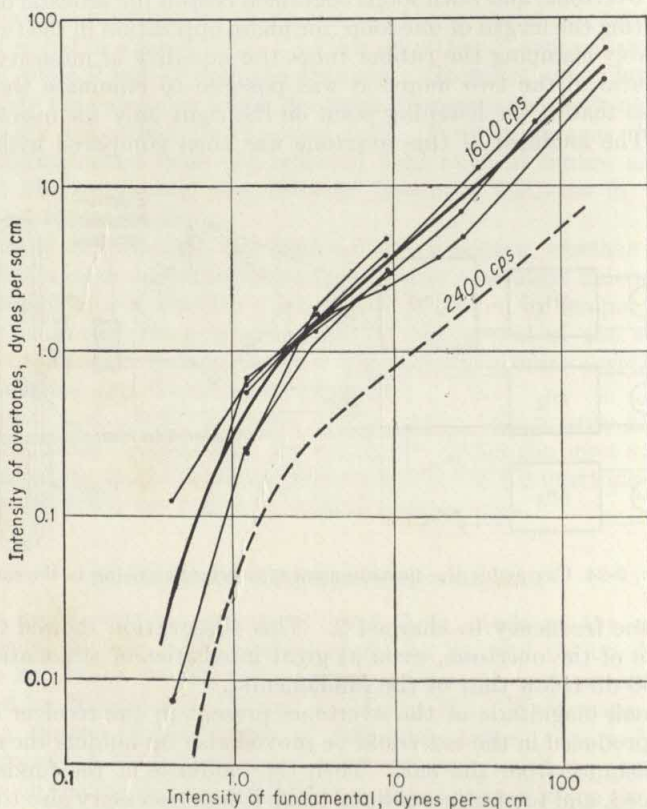


FIG. 9-25. Intensity of overtones for a fundamental of 800 cps.

abscissa, is presented in Fig. 9-25. The magnitudes of the harmonics are unexpectedly large. The second harmonic comes within 10 db of the amplitude of the fundamental. At the larger intensities the overtones vary almost in proportion to the fundamental, though at low intensities they change more rapidly. The results were similar for fundamental tones between 200 and 3000 cps. Thus in this region there is no systematic relation between the strength of the overtones and the frequency.

The following test was made to determine what externally arising overtones are perceptible in the presence of this great nonlinearity of the ear. A tone of 800 cps and a pressure of 1 dyne per sq cm was presented

along with a masking tone of 500 or 300 cps at an intensity of 3 dynes per sq cm. Then it was found how much the 800-cps tone had to be changed in intensity to produce a noticeable alteration of timbre. This amount was 6 to 10 per cent, which is approximately the difference threshold for 800 cps. If we designate as the distortion factor the ratio of the amplitude of the overtone to that of the fundamental, we find in general that for a pure tone of 400 cps at a sound pressure of 3 dynes per sq cm an increase of the distortion factor of 3 per cent is just audible. This figure is in agreement with the results of Janovsky (1), especially if it is borne in mind that here only one overtone has been considered rather than the total number.

The magnitudes of other overtones are shown in Fig. 9-26 for a tone of 200 cps at an intensity of 10 dynes per sq cm. These are all the overtones that are measurable for a tone of this magnitude.

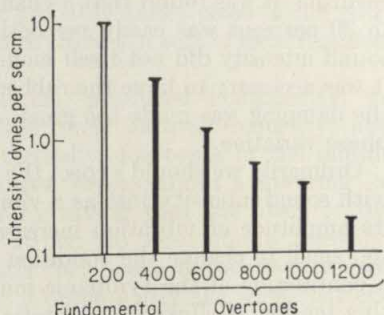


FIG. 9-26. Overtones arising in the ear on stimulation with 200 cps at an intensity of 10 dynes per sq cm.

Place of Origin of the Overtones. Next to be considered is in what part of the ear the overtones arise. To study nonlinearity of the vibrations of the eardrum, pure sinusoidal pressure variations were presented, and measurements were made of the overtones reflected from the drum surface. To produce pure tones an electrodynamic loudspeaker was followed by acoustic filters and a Quincke interference tube of the type already shown in Fig. 9-24. As already described, the branches just beyond the entrance to the Quincke system consisted of rubber tubes filled with cotton and adjusted with clamps to give equal intensities on the two sides. Then a suitable adjustment of the lengths of the two loops gave a cancellation of the tone at the listening point. A short side tube led off from the longer tube at a position about a quarter wavelength from the listening point, and this side tube was connected to the subject's meatus with a rubber tube. This system could be adjusted so that a fundamental tone presented at a high intensity to the meatus produced no audible effect at the listening point, yet any overtones arising in the meatus could readily be perceived. The damping afforded by the cotton in the rubber tubes was sufficient to prevent standing waves.

For a tone of 500 cps and a pressure of 10 dynes per sq cm there was no radiation of overtones from the eardrum. This means that overtones are not produced by the eardrum, for if they were they would have to be radiated. The ear was replaced by a telephone-receiver diaphragm that was made to vibrate at the frequency of the overtone and at an intensity at the small side tube of the Quincke system that would match the loudness of the subjective overtone. Then this tone was heard at the listening point at an intensity at least 40 db above threshold.

Because the eardrum vibrations are practically linear we should

expect the impedance of the eardrum to be independent of sound intensity. To test this point, the Quincke-tube system was adjusted for a minimum of tone at a high intensity, and then the intensity was reduced to a level 18 db above threshold. It was found that no further adjustments were necessary to obtain a minimum. If the meatus was replaced by a short closed tube of such a length as to require the same adjustments as the eardrum, it was found that a change in the impedance of the tube of 20 to 30 per cent was easily perceptible. To make sure that a change in sound intensity did not itself modify the adjustment of the tube system it was necessary to have the rubber tubes properly filled with cotton. If the damping was made too great, a change of intensity could produce a phase variation.

Ordinarily we should expect the impedance of the eardrum to increase with sound intensity just as a vibrating string is increased in tension as its amplitude of vibration increases. However, the vibrations may be too small to change the condition of tension of the eardrum. Likewise a contraction of the tympanic muscles seems to have little effect upon this tension (Geffcken). A static pressure of 6 cm of water, which is four times as large as the normal tension of the eardrum, produces only a 30 per cent change in the eardrum impedance.

That the overtones do not arise in the middle ear either is shown by the fact that a change of static pressure in the external meatus had no effect upon the magnitude of the overtones, provided that a compensation was made for the effect of the pressure upon the loudness of the fundamental and of the exploring tone by which the overtones were measured. The fundamentals used were of 250, 500, and 1000 cps at a sound pressure of 10 dynes per sq cm. Because the strength of the overtones depends merely on the intensity of the fundamental and not on conditions of tension in the eardrum and middle ear, it follows that the overtones are not the result of nonlinear distortion in the middle ear, but must arise for the most part in the cochlea.

This conclusion is supported by the following experiment. If a fundamental tone of 500 cps was used and best beats were produced with an exploring tone of 1004 cps, it was easily observed that a steady tone of 100 cps could be superimposed upon the beating overtone without any effect upon the purity and smoothness of the overtone. An overloaded vacuum tube does not act in this way. If the fundamental current is led to the grid of an amplifier tube and its voltage and the grid bias are adjusted so that the tube distorts and produces the same amount of overtones as the ear, the superposition of a 100-cps voltage even at very small values causes a modulation of the overtone at the rate of a hundred per second. The beating overtone then loses its smoothness and is changed to a beating "r" sound.

From this it follows that the nonlinearity of the ear cannot appear in the eardrum or the middle ear, for if it did there would have to be a simultaneous modulation of the tone just as in the nonlinear vacuum tube. The distortion can arise only in the cochlea, where the various tones have already become separated from one another. Each tone

operates upon a different nonlinear system, so that in spite of the fact that large overtones are present there cannot be any modulation. The appearance of strong combination tones is connected with this situation. This selective nonlinearity of the ear is due to the fact that the ear produces much less distortion of a tonal mixture than an ordinary transmission system with the same harmonic distortion.

The nonlinear distortion of the ear probably takes place in the eddy movements of the cochlear fluid, in which there is a sort of local rectification of the fluid vibrations.

If the fibers of the basilar membrane produced nonlinearity, an increase in sound intensity would alter their natural frequency, and there would be a change of pitch. Actually, for tones in the middle range of frequency, an intensity increase brings about a lowering of pitch. Zurmühl explained this effect by saying that the fibers of the basilar membrane, like a stretched string, do not vibrate linearly, because as their amplitude grows greater their mean tension is increased and their natural frequency is raised. Consequently the whole pattern of vibration on the basilar membrane is shifted toward the lower tones. Because it is easy to determine the pitch variations that arise from changes of sound intensity, the consequent nonlinearity of the basilar membrane should readily be determined.

Because we are only concerned with a rough value as a general indication, we can assume that the positive and negative variations of tension of a string are equal for a change of amplitude x . Then we can use Martin's equation

$$\ddot{x} = \alpha \dot{x} + \beta x - \gamma x^3 = K \sin \omega t \quad (9-2)$$

where $K \sin \omega t$ represents the driving force. If $f + \Delta f$ is the natural frequency of the system at an amplitude A , and f is the natural frequency at very small amplitudes, the increase in frequency with amplitude is

$$\frac{\Delta f}{f} = - \frac{3\gamma}{8 \times 4\pi^2 f^2} A^2$$

On the other hand, Timoshenko calculated that a vibrating system according to Eq. (9-2) would produce a large third harmonic A_3 whose amplitude relation to the fundamental is represented by

$$\frac{A_3}{A} = \frac{\gamma}{36 \times 4\pi^2 f^2} A^2$$

Hence we obtain $A_3/A = 0.074 \Delta f/f$. The change of pitch for a tone of 1000 cps and 10 dynes per sq cm is about 1 to 10 per cent (Zurmühl, Vrijdaghs); hence $A_3/A = 7 \times 10^{-4}$ to 7×10^{-3} . However, the measurements yield much larger values, and so this type of nonlinearity need not be considered.

Fatigue studies show that the overtones are not of neural origin but are purely mechanical.* In these studies strong fatiguing at the fre-

* See footnote, page 332.

quency of the fundamental tone produced a reduction in the loudness of this tone of more than 7 db. If overtones arose in the nervous system, the fatigue, because it is peripheral in nature, would weaken the overtones more than 7 db. This could not be observed, for the amplitude of the exploring tone that gave best beats remained at the same value after fatigue as before. In order to obtain the greatest possible decrease of loudness as a result of fatigue, the amplitude of the fundamental was reduced as much as could be done and still permit a precise measurement of the overtones.

Difference Tones Arising in the Ear. An arrangement for measuring the difference tones arising in the ear is shown in Fig. 9-27. With a tuned dynamic receiver F_1 against the ear, a primary tone of known sound pressure was produced by adjusting attenuator b_2 . A second

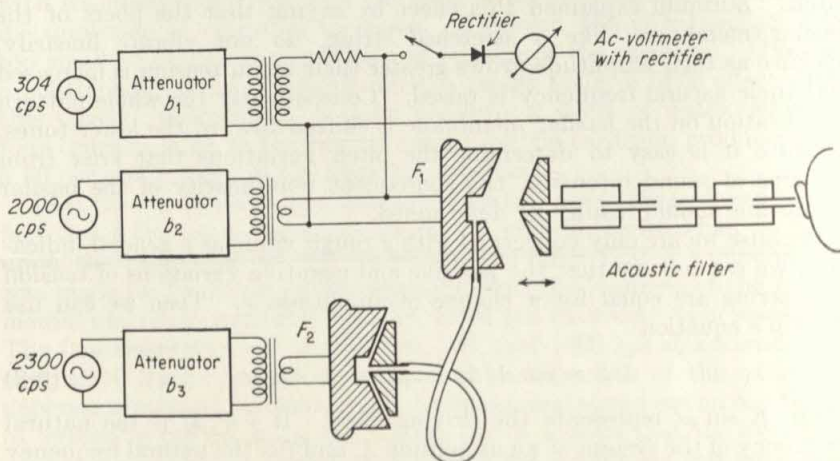


FIG. 9-27. Arrangement for measuring the difference tones arising in the ear and in the equipment.

primary tone was introduced into the ear through a rubber tube leading from a side opening in the receiver and was adjusted to the same sound pressure. An exploring tone was then added and its intensity adjusted to give best beats with the audible difference tone, and from a measurement of its voltage as applied to the receiver it was possible to determine the intensity of the difference tone.

If, as Fig. 9-27 shows, there is interposed between the receiver and the ear an acoustic filter that removes the primary tones, then the only difference tone that will be audible will be one produced in the equipment itself. If the exploring tone is again adjusted for best beats, the magnitude of this difference tone can be measured. The only precaution necessary here is that the diaphragm of the receiver have sufficient stiffness that its amplitude will not be changed when the acoustic filter is substituted for the ear.

Care was taken that in all the measurements the difference tone produced by the equipment was at least 20 db below that produced in the

ear. The two sound sources were isolated to prevent any mechanical interaction, and all connections were made airtight to prevent any jet effects through leaks. If instead of using two separate sound sources the two currents were superimposed upon the same receiver by means of a Wheatstone bridge, it was necessary to carry out frequent control tests. It was found that the difference tones produced by a newly purchased dynamic receiver were increased tenfold after two weeks of use. Also the difference tones measured in this way in a dynamic loudspeaker with a paper diaphragm often showed abrupt changes.

In Fig. 9-28 are shown the magnitudes of difference tones produced by two primary tones of 2000 and 2300 cps at the intensities shown on the

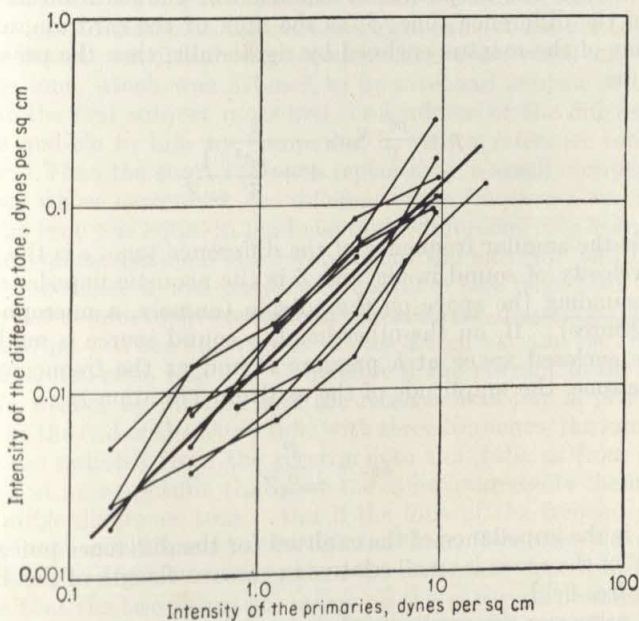


FIG. 9-28. Intensity of the difference tone as a function of the intensity of the primaries. The primary tones were 2000 and 2300 cps.

abscissa. It is seen that the difference tones were about 40 db weaker than the primary tones. For primary tones between 800 and 4000 cps and difference tones between 200 and 800 cps the results were exactly the same. When the difference tones were below 200 cps their magnitudes were greater, and at 100 cps they reached a value four times that indicated. This limited dependence on frequency for the difference tones was observed by Janovsky (1) in experiments of a different sort. If one of the primary tones was kept constant at 10 dynes per sq cm and the other was given various values as shown on the abscissa, the difference tone changed along a curve only a little less steep than shown here.

Primaries of high frequency and great intensity are reduced in loudness by fatigue to a greater extent than the low-pitched difference

tones, and therefore after prolonged observation the difference tone may seem louder relative to the primaries that would be expected from the data given here.

Place of Origin of Difference Tones. First to be considered in the determination of the place of origin of difference tones is the fact that the opening of the external meatus might act as a jet orifice in a free sound field in which the air might more easily flow in than out. However it was not possible, even at intensities near the threshold of feeling, to detect any air flow of this nature.

If the difference tones arose directly through asymmetry of vibration of the eardrum, then they also would be radiated externally to the meatus. If we take x_0 as the amplitude of vibration of the eardrum at the frequency of the difference tone, S_0 as the area of the eardrum, and V as the volume of the meatus enclosed by rigid walls, then the pressure p is obtained as

$$p = \frac{\rho c^2}{V} S_0 x_0 \frac{1}{1 + \frac{\rho c^2}{V} \frac{1}{i\omega Z}} \quad (9-3)$$

where ω is the angular frequency of the difference tone, ρ is the density, c is the velocity of sound in air, and Z is the acoustic impedance of the system bounding the space on the outside (namely, a microphone and a sound source). If, on the other hand, a sound source is made to act upon the enclosed space at a pressure P and at the frequency of the difference tone, the amplitude of the eardrum vibration is

$$x_0' = \frac{P}{i\omega S_0 Z_0} \quad (9-4)$$

where Z_0 is the impedance of the eardrum for the difference tone, and the volume V of the space is small relative to the wavelength of the difference tone in a free field.

If two primaries are applied and the sound pressure p is measured by means of the microphone in the enclosed space, then by Eq. (9-3) the amplitude of vibration x_0 of the eardrum can be calculated for the difference tone. If then instead of the two primaries a single tone is applied whose frequency and loudness are equal to the audible difference tone and its pressure P is measured with the microphone, the amplitude of the eardrum can be determined from Eq. (9-4). If the difference tone arises only in the eardrum, these two amplitudes will be the same, for in each instance the vibration is transmitted in the same way from the middle ear and inner ear to the auditory nerve.

If, however, the difference tone has its origin in the middle ear or in the inner ear, it is likely that the vibrations will not be fully transmitted to the eardrum. Then x_0 will be smaller than x_0' . Measurements were made with 2000 and 2300 cps at an intensity of 10 dynes per sq cm, and showed that the difference tone as observed at the eardrum had an ampli-

tude at least 20 db below that of an aerial tone of equal frequency and intensity. Therefore the difference tone does not arise through asymmetrical vibrations of the eardrum but in a further transmission of vibrations of the middle ear.

For the production of the two primary tones, two very stiff electrodynamic loudspeakers were used, of which one was used as a microphone and the other as a source for the 300-cps tone. By closing the volume V with a rigid plate instead of the eardrum it could be shown that no difference tone arose in the equipment itself.

The radiation of difference tones by the eardrum was investigated by another method also. A short tube with three branches was attached to the eardrum. Two of the branches served to conduct the two primary tones from two separate sound sources by means of rubber tubes. To the third branch was attached an acoustic filter that would only pass the difference tone, which was listened to by a second subject at the same time that the first subject measured the loudness of the difference tone that was audible to him by comparing it with a reference tone in the other ear. Then the short tube was replaced by a small receiver of high impedance whose current at the difference-tone frequency was adjusted so that the tone was equal in loudness to the difference tone heard earlier. From the volume between the receiver and the eardrum and from the eardrum impedance it was possible to calculate (see page 136) the ratio between the volume displacement of the receiver diaphragm and that of the eardrum. When the volume V was 3.5 cu cm and the frequency was 250 cps this ratio was 2.7. Therefore if the current to the receiver was made weaker by 2.7-fold and the receiver was put in place of the eardrum at the end of the short tube with three branches, the same sound mixture was radiated from the receiver into this tube as from the eardrum, and at an amplitude that gave the same loudness to the inner ear as the audible difference tone. But if the tone of the frequency of the difference tone was listened to through the filter, it became clear that it was at least 10 to 18 db stronger than the difference tone heard before. It follows that the two primaries acting on the eardrum produced a difference tone that was at least 10 to 18 db below the amplitude of an ordinary tone with the same frequency and loudness.

To study the part played by the middle-ear apparatus in the production of difference tones, a positive or negative static pressure of a few centimeters of water was introduced into the external meatus. Then the eardrum and ossicles were displaced and twisted away from their normal positions, with changes in the tensions and pressures in their articulations and in the tendons that anchor them to the temporal bone. If the difference tones arose in these connections they would be altered by this procedure.

To carry out these measurements, two small loudspeaker systems were enclosed in an airtight chamber, with one opening into the meatus and another opening to a pressure system. The changes of loudness observed by a subject for three different pairs of primary tones, together with their difference tones, are shown in Fig. 9-29. Also shown are the loud-

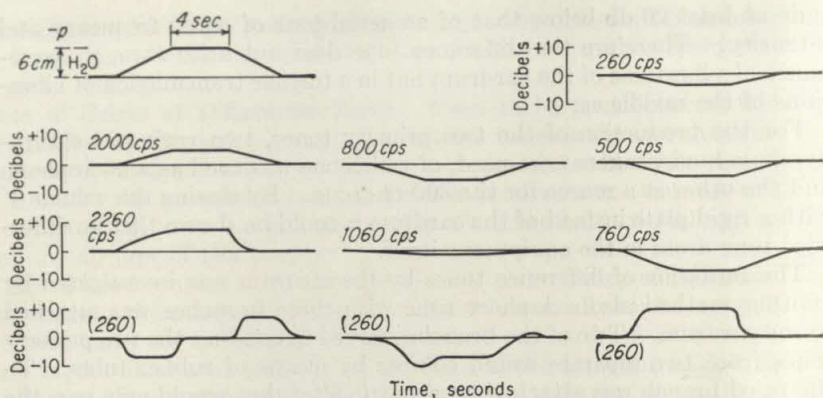


FIG. 9-29. Loudness changes in the primaries and their difference tone caused by a static pressure variation in the external meatus.

ness changes observed in a normal tone of 260 cps, which is the same frequency as the difference tone.

The static pressure change consisted of a negative pressure of 6 cm of water, which was raised from zero to its final value in about 4 sec.

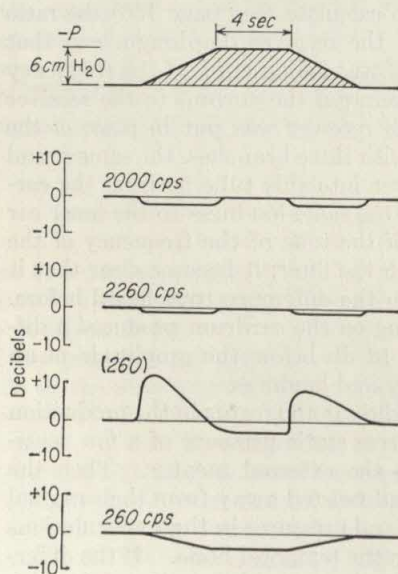


FIG. 9-30. Results as in the preceding figure, for another subject.

The course of the curves varied greatly with the frequency of the primary tones. Often they were reproducible over long periods, and then suddenly they underwent large changes. They were different for every subject, as a comparison of Fig. 9-30 with Fig. 9-29 will show, but there were only slight variations between the two ears of a given subject. In Fig. 9-30 the loudness changes arise, it seems, only as the pressure is rising or falling. In this subject the loudness changes became much greater when the static pressure was altered rapidly. Instead of introducing the static pressures into the meatus in this manner, it is possible to suck out some of the air of the middle-ear cavity through the Eustachian tube at the moment that it is opened during swallowing. One way to do

this is to swallow while holding the nose.

Even in the tests in which the static pressure changes had no noticeable effect upon the transmission of the primary tones to the cochlea, the loudness of the difference tone became about 10 db greater, and for

larger pressures more than 20 db greater. From this it follows that to an important extent the difference tones arise in the middle ear. This conclusion is supported also by the fact that the static pressure not only affects the loudness of the difference tones but also changes the form of their dependence upon the intensity relations of the primaries.

If the static pressure in the meatus is made to last for a long time, rather than just a few seconds, it is found that even after some minutes the changes of loudness have not yet reached a final value. Figure 9-31 shows results obtained for two tones of 1000 and 1226 cps, each at 60 db above threshold, when a negative pressure of 6 cm of water was continued for 15 min. The temporal course of the loudness changes in the difference tone are shown. After the static pressure was removed there was a large aftereffect. This aftereffect is in part responsible for the fact that the measurements are difficult to reproduce. There is a significant increase

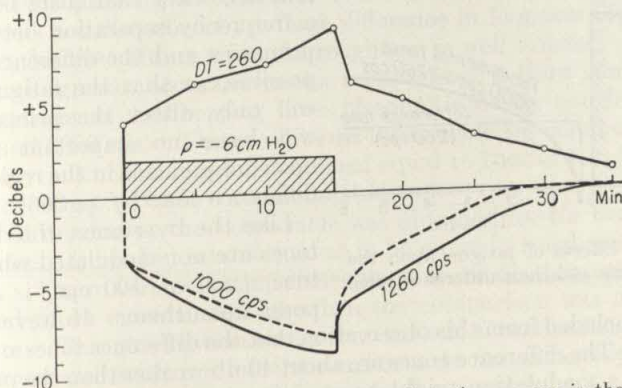


FIG. 9-31. Aftereffects caused by a long-continued static pressure in the meatus.

in the loudness of the difference tone during the time the negative pressure is continued, especially when we consider that the primary tones have been reduced.

After it was found that pressure changes in the meatus produced large changes in the difference tones, a study was made of the effects of tensor contractions. A difference tone was produced in one ear by applying the weakest possible primaries, and in the other ear a tone of 3000 cps at 10 dynes per sq cm or over was introduced in order to evoke tensor contractions in both ears. When this tone was introduced there was, usually a momentary reduction in the strength of the difference tone, but after a second this effect was reduced to about 1 db at most. When the 3000-cps tone was removed there was a considerable overshooting of the loudness of the difference tone. The loudness changes produced by a static air pressure in the meatus had a different course, and therefore it appears that a tensor contraction produces different sorts of alterations of the ossicles.

The following evidence proves that the difference tones, like the overtones, have a purely mechanical origin. The ear can be fatigued for a

long time with a strong tone of a frequency close to that of the primaries, so that after the fatiguing tone is removed the primaries are largely inaudible. Then the primaries only regain their loudness gradually as the ear recovers in the course of time, and finally reach a terminal value. Because the fatigue acts upon the nerve endings, it would be expected that if the difference tones had a neural origin their loudness would rise as the nerves recover. This does not happen. As Fig. 9-32 shows, the difference tone after fatigue has a loudness of constant value, despite the fact that the primary tones are rising during a period of several seconds. Therefore the difference tone is produced at an entirely different place on the basilar membrane from the primary tones. It must arise in a mechanical way in the middle ear or in the cochlea, and then it stimulates the basilar membrane at its proper place just like any other tone.

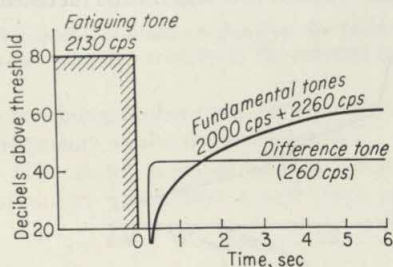


FIG. 9-32. Effects of fatigue upon the fundamentals and their difference tone.

For the success of this experiment it is necessary that there be as large a frequency separation between the primaries and the difference tone as possible, so that the fatiguing tone will only affect the primaries and will have no important influence upon frequencies in the region of the difference tone (*cf.* p. 366).

Like the overtones, the difference tones are not modulated when a low tone, such as 100 cps, is superimposed upon them. However, it cannot be concluded from this observation that the difference tones arise in the cochlea. The difference tones are about 40 db weaker than the primaries, and thus a modulation might be present without being noticed. More significant is the fact that the difference tones depend upon the conditions of tension in the middle ear. They do not arise in the cochlea, as the overtones do, but in the middle ear, and apparently in the vibrations of the stapes. Therefore the difference tones and overtones arise at different places in the ear. Only on this basis can we understand why the difference tones do not have the same order of magnitude as the overtones. The basilar membrane can give rise to the difference tones only when they have very low frequencies—below 200 cps—where they become large in magnitude. Then they arise because the primary tones on the basilar membrane are no longer widely separated from one another. A further clarification of this problem is to be expected from a study of fluid vibration and streaming in a model of the ear.

ACOUSTIC ROUGHNESS*

The nonlinear distortion of speech and music gives rise to overtones, combination tones, and a type of roughness due to beats and a modulation

* Article 21 as listed in the Author's Bibliography. Published in 1935.

of the primary sounds. This roughness is an important and a particularly disturbing aspect of the distortion, and it will first be examined in its simplest manifestations in tones and clangs. This study will provide a basis for its further consideration in speech and music.

Measurement of Roughness. Experiments were carried out to discover the extent to which the quality of roughness can be distinguished from other auditory attributes, such as loudness, volume, brightness, and the like, and to measure the accuracy with which two different kinds of roughness may be compared. In this comparison, two different modulated tones were used. One was a 200-cps tone modulated 100 per cent at a rate of fifty times per second, and the other was a 500-cps tone modulated at the rate of ninety times per second to an extent just sufficient to give observable roughness. These two tones could be adjusted to the same amount of roughness by a considerable reduction in the sound pressure of the first tone. This adjustment for equal roughness is not disturbed by a large difference in loudness between the two tones, because after a time the roughness is well isolated.

To obtain greater accuracy in this comparison, a third stimulus was used, consisting of two beating tones of equal intensity and frequencies of 3000 and 3050 cps. These combined tones could be raised or lowered in intensity until their roughness seemed equal to that of one of the two modulated tones. If the two modulated tones were first adjusted for equality of roughness, the same value was obtained for the beating tone when it was adjusted in intensity so as to be equal in roughness to either of these. There were sometimes variations of 10 db, but usually they amounted to no more than 3 db when the comparison was made with great care. This observation shows that various sensations of roughness can be compared with a standard roughness in the same way that the loudness of a noise is measured in terms of a normal tone. However, the attribute of roughness is not as basic as loudness is, and its measurement imposes a burden on the subject much like that of analyzing a tone out of a complex sound. It is therefore understandable that not every subject can perform equally well. Therefore it was necessary before every extended series of measurements to carry out a control series in which two different roughnesses of equal intensity were compared with a third. In this way the subject's error of observation was obtained.

As a standard roughness the beating tones of 3000 and 3050 cps were used, and this roughness was varied by simultaneously altering the intensity of the two tones. As a quantitative indication the absolute sound pressure in dynes per square centimeter at the beat maximum was used. This standard is easy to produce, and the amplitude variations of these tones give a wide range of roughness. The beat rate was chosen as fifty per second because at this frequency there is little disturbance by the difference tone. Also this rate of beating gives roughness of a somewhat intermediate character, lying between that of slower rates, which is of an "R" character, and that of higher rates, which is of a "Z" character.

Roughness Produced by Two Simultaneous Tones. If a pure tone of 200 cps and a constant intensity of 10 dynes per sq cm is added to a second tone of the same frequency and intensity and then the second tone is gradually raised in frequency, there first appear slow beats whose variations of loudness are easily followed. When the second tone reaches about 220 cps the combination begins to take on an "R" character, and as the frequency is raised further the roughness first increases and then declines. Around 290 cps the roughness is still present, and it is not possible to separate the two tones. This fact is indicated schematically in Fig. 9-33. Here the upper broken line represents the constant tone of 200 cps, and the lower broken line represents the tone whose frequency is varied. The perceived roughness is indicated by the black area between these two lines. In the region of 300 cps this relation changes, for the variable tone is now separable from the rough complex, and is heard as slowly beating. At the same time there is the impression that

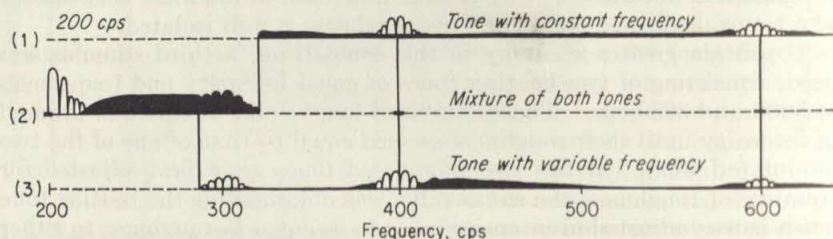


FIG. 9-33. Schema representing the roughness arising from two simultaneous tones of equal intensity.

the rough complex is modulated at the rate of the beating. At 320 cps the two tones can be separated. The variable tone seems to be completely isolated and smooth, while the 200-cps tone has a certain roughness. This roughness declines as the variable tone is further increased in frequency. In the region of 400 and 600 cps the two tones usually are heard as separately beating, and to the right and left of the beating there are minor increases in the roughness. Just at 400 cps and 600 cps the two tones fuse to an unanalyzable complex.

These phenomena sometimes show variations from the description given, because subjects vary greatly in their ability to analyze a tonal mixture. Thus it is difficult to determine the frequency separation of the two tones that is necessary to make them individually audible. It is also difficult to determine the separation at which the roughness disappears, especially when there is disturbance from the difference tone.

The following experiments were carried out to discover whether the rate of beating at which roughness disappears depends upon the pitch. Three tones were used, of 200, 800, and 3200 cps, and the dependence of roughness upon the beating rate was measured. The results were highly consistent, and are shown in Fig. 9-34. The two beating tones always had an effective sound pressure of 10 dynes per sq cm. The beating rate, produced by raising one of the tones in frequency, is shown on the

abscissa. The ordinate shows the equivalent roughness in terms of the standard.

The measurement of roughness as a function of pitch could be carried out most simply by switching back and forth between the standard and one of the three beating tones and thus making direct comparisons. However, this procedure calls for six oscillators that are free of overtones. To avoid this requirement, a fluid potentiometer like that described by E. Meyer and Keidel was used.

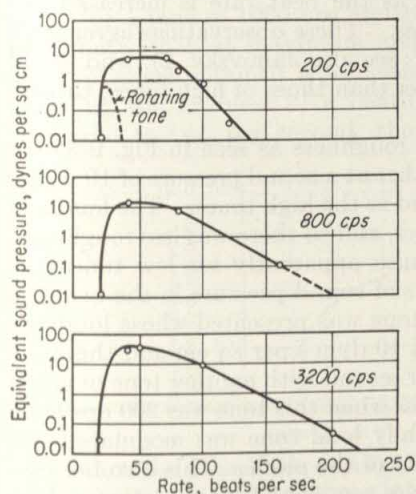


FIG. 9-34. The roughness of beats as a function of beating rate and tonal frequency.

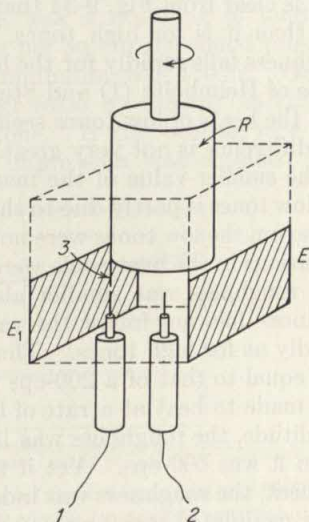


FIG. 9-35. A fluid potentiometer for the generation of beats and modulated tones.

If p and q represent the frequencies of two beating tones, then

$$\sin 2\pi p t + \sin 2\pi q t = 2 \cos 2\pi \frac{p - q}{2} t \sin 2\pi \frac{p + q}{2} t$$

This equation shows that the beats can be obtained in another way, if the amplitude of a single tone whose frequency is $(p + q)/2$ is varied in proportion to the cosine of half the beat rate. This was done by means of a square trough of insulating material filled with a conducting fluid, in whose lower half there were two electrodes covered with platinum black as shown in Fig. 9-35. A tone of a frequency $(p + q)/2$ was conducted to these electrodes. The potential difference arising between electrode 2 and a probe 3 attached to the rotor R was led to the grid of an amplifier tube, and gave a beating tone. The beating rate was twice the frequency of rotation of the rotor. If the trough was made narrower than 8 mm it was possible to obtain beats faster than 150 per second. The fluid was a solution of sodium chloride, and the trough and rotor were made of pure bakelite, which is unaffected by the fluid.

If electrode 1 was used instead of 2, and 1 was situated on the line of intersection of the rotor *R* with the plane of the trough perpendicular to the electrodes, then the potential difference between rotating and fixed probes was zero at only one point during a complete rotation. Then the tone was 100 per cent modulated. To obtain a smaller degree of modulation, a resistor was inserted in series with the electrodes and the potential was led off from probe 3 and some point on the resistor. Varying the position of contact with the resistor controlled the degree of modulation.

It is clear from Fig. 9-34 that for low tones the maximum roughness is less than it is for high tones. Also, as the beat rate is increased the roughness falls rapidly for the low tones. These observations agree with those of Helmholtz (1) and Stumpf (1; see also Janovsky, 2), who found that the beats of low tones seem weaker than those of high tones, though the difference is not very great.

The smaller value of the maximum roughness as seen in Fig. 9-34 for the low tones is partly due to the fact that at a sound pressure of 10 dynes per sq cm the low tones were not as loud as the high tones. The loudness variations in the beat cycle were smaller, and so there was less roughness. The roughness was smaller also because apparently for low tones the loudness does not follow the variations of sound pressure in the beats as rapidly as for high tones. Thus if a tone was presented whose loudness was equal to that of a 200-cps tone at 10 dynes per sq cm and this tone was made to beat at a rate of fifty per second with another tone of equal amplitude, the roughness was 10 db less when this tone was 200 cps than when it was 600 cps. Yet if the equally loud tone was modulated 100 per cent, the roughness was independent of the pitch. This is so because for a modulated tone the sound pressure remains at its minimum values for a much longer time than it does for beats (*cf.* Waetzmann, 5).

With beats it is possible also to obtain a temporal course of pressure amplitudes like that for a modulated tone. This is the case when the amplitude of one of the tones is much smaller than that of the other. A large number of observations showed that an amplitude ratio for the beating tones below 1:2 (giving a sound-pressure variation at the maximum that was not over three times that at the minimum) gave the same amount of roughness for all tones from 200 to 4000 cps, provided that for equal loudness the sound-pressure changes and the beating rate were the same. But if the sound-pressure variations were smaller than 20 per cent, so that the roughness approached its threshold, these relations no longer held (see Riesz, 1; Beljers; Janovsky, 1).

The falling off of roughness with the reduction in the amplitude of a tone is shown in Fig. 9-36. Here one of the tones, of a frequency of 800 cps, was at 10 dynes per sq cm, and the other, with a frequency of 850 cps, was varied in intensity as shown on the abscissa.

It is to be expected that the roughness can be calculated from the changes of sound pressure and the resulting loudness changes, which may be obtained from equal-loudness functions. Yet the sensations of roughness are only loosely connected with loudness variations. For a constant variation in loudness the roughness declines as the loudness

level falls. The decline is proportional to the fall in loudness level if the standard loudness is a tone of 1000 cps. There are large individual differences, however.

The peculiar transformation of loudness variations into roughness could readily be followed if the amplitude ratio between two beating tones was selected so that the loudness variations seemed equal to the constant background tone, or in other words, when the sound-pressure maximum gave just twice the loudness of the sound-pressure minimum. For beats of about 0.5 cps, for which a direct comparison could be made between maximum and minimum, there was a doubling of loudness when for a tone of 1000 cps and 10 dynes per sq cm the sound pressure ratio between beat maximum and beat minimum was 1:0.57. Geiger and Firestone obtained a somewhat larger ratio by directly halving or doubling the loudness of a continuous tone. If the beating rate was increased to two per second, the usual impression was obtained of a

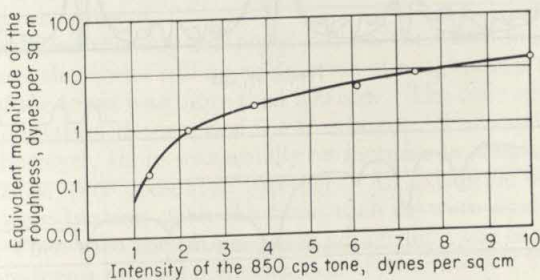


FIG. 9-36. Effect of amplitude on roughness. One of the beating tones was 800 cps at 10 dynes per sq cm, and the other was 850 cps at various intensities as shown on the abscissa.

loudness maximum as a separate pulse, and the variations of loudness were greatly overestimated. Then a sound-pressure ratio of 1:0.76 gave loudness variations that seemed equal to those of a constant, steady tone. When the beating rate was increased further the loudness variations seemed to run together, and at fifty per second a sound pressure of 1:0.33 was required. In order to obtain a roughness equal to the underlying constant tone with a tone of 200 cps and a rate of fifty beats per second it was necessary to make the amplitudes of the two beating tones equal, for the beats already were running together so that the sound pressure had to fall to zero.

If the two beating tones were not led to the same ear but were presented separately to the two ears, the beating was not heard. Instead there was a rotating tone (Hornbostel, 1). If the frequency difference was below 1 cps, it was easy to observe how the apparent locus of the sound rotated about the head, but without any alteration in its loudness. If the rate of rotation was increased, however, the spatial variation of the sound of rotation was changed into a loudness variation. For a frequency difference of 20 cps there was a clear sensation of roughness, whose magnitude is indicated by the broken line at the top of Fig. 9-34 for a tone of 200 cps

and 10 dynes per sq cm. When the frequency difference was further increased the roughness decreased sharply, and the two tones were heard as separate in the two ears. The roughness fell off rapidly as the pitch of the rotating tone was raised.

Roughness of Two Simultaneous Tones, and the Addition of Two Roughnesses. If two beating tones are not absolutely pure, but contain a series of overtones, then in general the roughness of the complex is less than that of two pure tones of the same sound pressure. This fact was best observed by using clangs with low-frequency fundamentals and switching a filter in and out of the earphone circuit. The decrease in roughness results from the fact that the beating of the overtones is

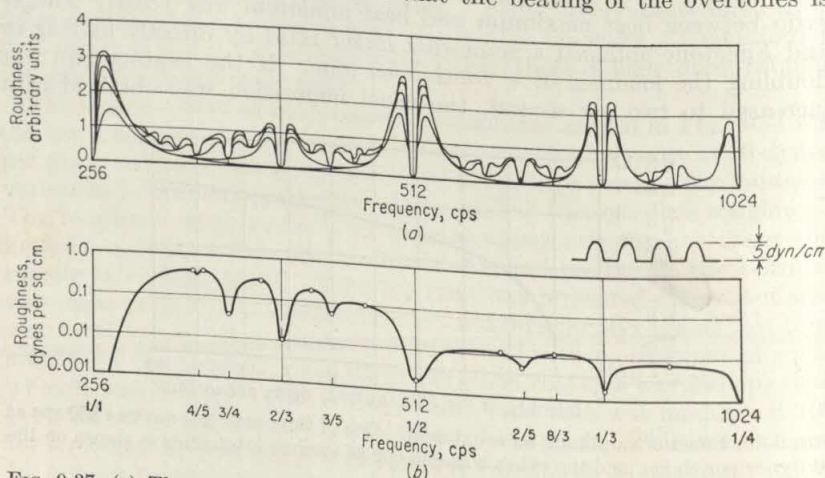


FIG. 9-37. (a) The roughness of two violin notes, one at 256 and the other varying from 256 to 1024 cps, as calculated by Helmholtz. The ordinate scale is arbitrary. (b) Measurements of roughness over the same range. The lower scale is in dynes per sq cm.

not in phase with that of the fundamental, so that the abrupt falling off in loudness in passing through a minimum is filled in by overtones. On the other hand, the roughness extends over a much greater range of beating than it does for pure tones.

Helmholtz (1) calculated how the roughness of two violin notes ought to change when the fundamental of one was held constant at 256 cps and another note of equal intensity was progressively raised from 256 to 1024. The upper portion of Fig. 9-37 shows the magnitude of the roughness on an arbitrary scale. There are sharp minima of roughness at certain frequency ratios. These results were used as a basis for a theory of consonance.

The relation of roughness to frequency was measured for two rectified sine waves with a maximum pressure of 5 dynes per sq cm. These results are shown in the lower part of Fig. 9-37. Similar curves were obtained for other clangs also. For the larger valleys in this curve there is good agreement with Helmholtz's calculations. The steeper forms of the

maxima of the calculated data were obtained because Helmholtz assumed that the maximum roughness occurs at a beating rate of thirty-three per second and that the roughness falls off on both sides of this maximum at a greater rate than the measurements showed. Also it is to be noted that one ordinate is logarithmic and the other is linear. Moreover roughness arising from the various kinds of beats are simply superimposed in order to obtain this general indication, whereas in fact they are probably not additive.

Thus if a tone of 1000 cps was superimposed on another tone of 1070 cps and half the sound pressure of the first, the roughness was not increased if these beats were weakly modulated with 30 cps. What was heard was a "Z" type of beating modulated with 30 cps. For strong modulation the roughness was just as great as when a smooth tone whose sound pressure was the same as that of the beats was completely modulated. Thus the roughnesses do not add, but the total roughness is equal to the largest roughness present.

If the roughness was superimposed not on the same tone but on two different tones, there was still no summation of roughness if the frequency separation of the tones was more than 200 cps. The tone with the highest degree of modulation determined the roughness. For smaller frequency separation, however, there was usually an increase in roughness when the two rough tones were presented together. An exception occurred when both tones were beating with the same tone or were modulated at the same rate. Then with the proper phase adjustment the beats or modulation could produce a mutual compensation of roughness. This effect was best observed by simultaneously presenting the four tones $800 + 830$ and $900 + 931$, whereupon there was a prominent reduction in the roughness once per second at the moment of the beating of the two beats.

Roughness of Pure Tones. Even pure tones present a certain amount of roughness. A tone of a frequency beyond 3000 cps seems completely smooth and shows a certain similarity to the steady pressure of a needle in contact with the skin. But if the frequency is lowered it is clearly noted that a tone of 1000 cps is not as smooth as one of 3000 cps. For tones below 3000 cps the roughness can usually be clearly distinguished. The lower curve of Fig. 9-38 shows the moderate degree of roughness obtained for pure tones of an effective pressure of 5 dynes per sq cm. Unfortunately these measurements are not readily reproducible, and there are large individual differences among subjects. These differences are not due to errors of observation, for an intercomparison of three equal roughnesses gives a much smaller dispersion of data. Nevertheless it is clear that the low tones always approach an impulsive character. Overtones arising in the ear are partly responsible for these effects, for as the frequency falls these overtones become louder relative to the fundamental tones.

These overtones can be made greater by using square waves of ± 2.5 dynes per sq cm. Then the roughness is greatly increased, as the upper curve of Fig. 9-38 indicates. Beyond 300 cps the roughness is not measurable. At 50 cps, however, the clang complex already seems

completely modulated, for a series of clicks does not become any rougher when the frequency is reduced further.

Relations between Rough and Pure Tones. According to a simple place theory every tone has a narrowly limited region of action on the basilar membrane. When two tones are acting at the same time they will interact only in the regions adjacent to one another, and the exterior regions of action of the two remain largely undisturbed. On such a theory it is to be expected that the region of action of two beating tones will be only a little larger than the general regions of the individual tones. Hence such attributes of the tones as the difference threshold and masking will remain unchanged. This could be proved experimentally for tones that were made to beat with 50 cps. Down to 200 cps the curves of equal loudness for both tones remained the same, and also the forms of the masking curves as a function of frequency were unaltered. This

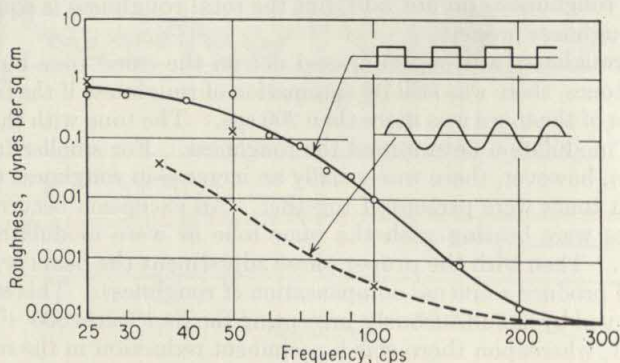


FIG. 9-38. The roughness of square waves (solid line) and of pure tones (broken line).

was true regardless of whether the rough tone was made to mask the smooth tone or vice versa.

However, there is an important difference in regard to fatigue phenomena. Thus if the ear is exposed to a strong tone of constant sound pressure, the loudness of this tone declines continuously with time (page 357). It is now to be expected that this fatigue of the auditory nerve will be smaller for a beating tone than for a steady tone, because for the beating tone there will be times during the decreased periods for the nerve to recover (Helmholtz, 1).

Only 80 per cent of the subjects showed this expected difference, though for them the difference was very large. The solid curve of Fig. 9-39 shows the fatigue effect of a tone of 1000 cps and an intensity of 10 dynes per sq cm in relation to the duration of fatigue. The measurements were carried out by presenting the fatiguing tone to one ear and then at the end of the fatiguing period presenting to the other ear a tone pulse 0.3 sec long and with a sound pressure p_1 that was adjusted so as to seem of the same loudness as the fatiguing tone. The relation between this sound pressure p_1 and the pressure p_2 of the fatiguing tone of 0.3 sec that seemed equally loud was expressed in decibels. If now to the tone

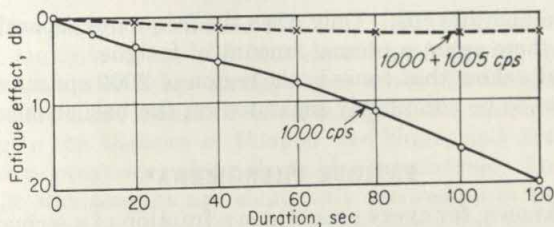


FIG. 9-39. The fatigue effects of a simple tone (solid line) and of a beating tone as a function of duration.

of 1000 cps was added a 1005-cps tone of equal sound pressure, then the fatigue was much less than that shown by the solid curve, even though the maximal sound pressure now was twice as great as for the smooth tone.

If the beat frequency was increased, the fatigue became still smaller as Fig. 9-40 shows, because for this subject no fatigue was demonstrable for beat frequencies above fifteen per second. For the pure tone, however, there was a fatigue of 33 db.

These effects are often of importance for measurements of loudness that are carried out over an extended period of time. Thus if instead of the usual pure tone of 1000 cps a beating tone of 1000 and 1050 cps is used as a standard of loudness, most subjects show much less dispersion of the observations as a result of fatigue.

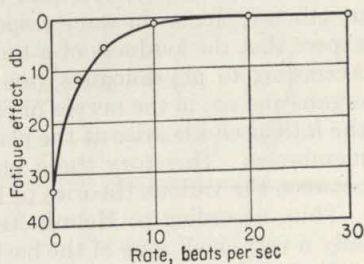


FIG. 9-40. Effect of beating rate on fatigue. The duration of the fatigue was 2 min.

If the frequency separation of the two beating tones is steadily increased, the two tones are finally heard as completely separate. Then the roughness falls off greatly, and the two tones again show their normal amounts of fatigue.

In Fig. 9-41 these effects are represented. At 2000 cps is shown in decibels the fatigue effect of a pure tone of 2000 cps at an intensity of 10 dynes per sq cm and a duration of 1 min. If to this tone was added another of equal sound pressure and with a frequency as shown on the abscissa, the fatigue disappeared almost completely until the frequency

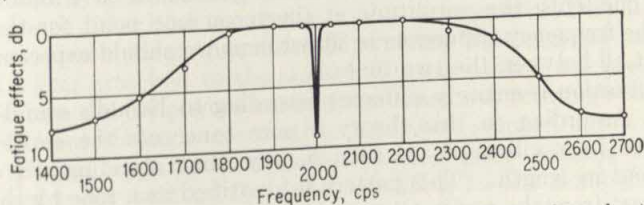


FIG. 9-41. Effects of frequency separation on the fatigue effects of two beating tones. One tone was maintained at 2000 cps, and the other was varied in frequency as shown on the abscissa.

separation became 200 cps. Only when the frequency separation reached 600 cps was there again a normal amount of fatigue.

These results show that tones in the region of 2000 cps must be 600 cps apart in order to be completely separated on the basilar membrane.

FATIGUE PHENOMENA*

As is well known, for every sense organ a fraction of a second is required after a stimulus is suddenly introduced at constant intensity before the sensation can attain its full value, and then after a few seconds have passed the sensation declines from this maximum as a result of fatigue. These relations for the sense of touch have been investigated by von Frey and Goldman. They showed that the pressure sensation aroused by placing a small weight upon the skin was reduced by fatigue to a magnitude three-fifths to one-fifth of the maximum within 3 sec, the reduction varying according to the size of the weight and the surface stimulated.

Because sensations of sound are produced by pressure on the basilar membrane, similar in some respects to the pressure on the skin, we may expect that the loudness of a tone will fall off in time because of fatigue. According to physiologists (see von Frey), fatigue arises in the sense organs and not in the nerves or central nervous system. Thus for sounds the fatigue effects arise at the places of pressure stimulation on the basilar membrane. Therefore these phenomena may be used to discriminate between the various theories of hearing.

Thus, according to Helmholtz's resonance theory, a pure tone affects only a very small zone of the basilar membrane. Only here will the nerve endings suffer fatigue. Therefore, if after a certain time the frequency of the tone is changed by a small amount, the place of stimulation on the basilar membrane will be altered only a little from the foregoing, and many of the same nerve fibers will be stimulated that have already been subjected to fatigue. Consequently the loudness of the second tone will be impaired. On the other hand, if the frequency difference is greater so that entirely different elements of the basilar membrane are stimulated whose nerve fibers are unfatigued, there will not be any weakening of the second tone.

If we take the commonly accepted value of 0.1 as the logarithmic damping of the cochlear resonators, then an element whose natural frequency departs by 15 per cent from that of a given tone will have an amplitude of only one-tenth the amplitude at the resonance point for that tone. When the frequency difference is 30 per cent we should expect no interaction at all between the two tones.

The situation is entirely different according to Ewald's sound-pattern theory. According to this theory a pure tone sets the entire basilar membrane into vibration in such a way that standing waves arise throughout its length. This pattern is identified as a tone by the brain. Since apart from the nodes all regions of the membrane are fatigued, we should expect that any succeeding tone whatever would have its loudness

* Article 3 as listed in the Author's Bibliography. Published in 1929.

reduced. The fatigue would be less only for tones whose frequency was an odd multiple or an odd fraction of the fatiguing tone, for such tones would have their loops at the places where the fatiguing tone had nodes and where there would be no fatiguing of the endings.

According to the theories of Bonnier, ter Kuile, and Max F. Meyer, a damped wave progresses along the basilar membrane. For high tones, for which the wavelengths are short, only the region in the vicinity of the stapes is involved, whereas for the low tones, for which the wavelengths are long, the wave stimulates a larger region of the membrane. Therefore a second tone of a frequency higher than that of the fatiguing tone will show the fatigue strongly, whereas one of a frequency lower than the fatiguing tone will show only slight effects.

As will be seen, the fatigue phenomena provide crucial evidence in relation to the various theories of hearing. In addition, they are of interest in acoustic measurements because they show to a large degree the individual differences among subjects.

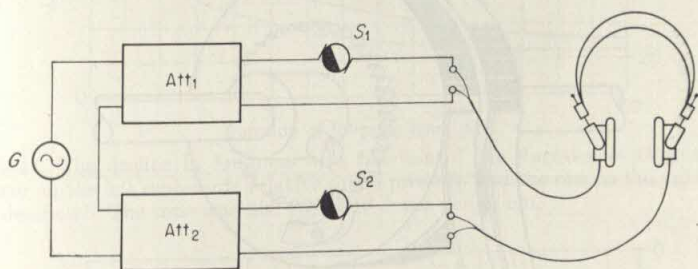


FIG. 9-42. Circuit for measuring loudness as a function of the duration of fatigue.

Fatigue Phenomena. To determine how loudness changes in time for a constant tone, the circuit of Fig. 9-42 was used. Oscillator *G* worked into two attenuators *b*₁ and *b*₂, which led through interrupters *S*₁ and *S*₂ to a pair of telephone receivers, one on each ear. The attenuators regulated the loudness of the tones and had sufficient damping that the opening or closing of the interrupter had no effect on the oscillator current (Breisig).

The interrupters served to present the tones at certain intervals of time. As may be seen in Fig. 9-43 they consisted of two disks, each half enclosed by a metal ring mounted on the same shaft. The circuit was completed if both of the springs made contact with the metal ring at the same time. Each disk also had a ratchet that engaged numbered teeth on a gear attached to the shaft. When a button was pressed the shaft as shown was coupled to another shaft that was rotating at constant speed. It went through one rotation and then stopped automatically. (An old Hughes apparatus, made for a telegraphic printing machine, was utilized.) By setting the disks according to the numbered teeth and making a proper choice of the speed of the shaft by means of the gear system, the time the tone would come on after the button was pressed, and also the duration of the tone, could be determined.

The time relations required by the following experiments were obtained by using three sets of these disks mounted on a common shaft. The interrupter was arranged so that a long-continued fatiguing tone was produced by one receiver, and another receiver on the other ear produced a tone of 0.2 sec duration just after the fatiguing tone ended. This second tone was adjusted in intensity by means of an attenuator so as to have the same loudness as the terminal portion of the fatiguing tone. It was found that as the duration of the fatiguing tone was increased the test tone had to be made weaker.

For the data to be reproducible it was necessary to follow each presentation with a considerable interval, which amounted to 3 to 8 min according to the duration of the fatiguing tone.

Figure 9-44 shows the variation of loudness with duration for an 800-cps tone at an intensity of 10 dynes per sq cm. The ordinate indicates the

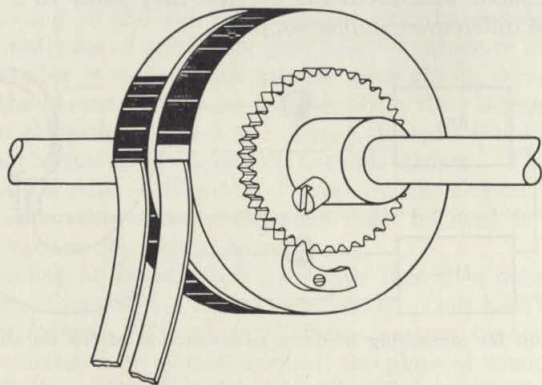


FIG. 9-43. Construction of the interrupter.

loss of loudness in decibels as a result of fatigue. The solid curve represents the mean values obtained for ten subjects, and the broken curves above and below it represent the smallest and largest effects observed. It is obvious that there are large individual differences in the effects of fatigue.

The fatigue effect varies greatly also as a function of the intensity of the fatiguing tone. This is shown in Fig. 9-45 where the results are given for 800 cps at intensities of 2, 10, and 50 dynes per sq cm, and for a subject exhibiting average fatigue effects.

On the other hand, the fatigue effect bears only a slight relation to frequency over the range used, which extended from 300 to 8000 cps, when the intensity is maintained at 10 dynes per sq cm. This remains true for a complex tone or a noise, such as was produced by a rapid interruption of the 800-cps tone. For this noise the fatigue effect was the same as for a tone if its loudness was made the same, as determined by direct comparison. However, when other sorts of noises were used, in which there were large momentary variations of intensity, the fatigue effect was smaller than for a tone of the same loudness. For example,

in one test the loudness of a tone declined 10 db whereas that of speech declined only 1 db. This effect plays an important part when the loudness of speech is being compared with a standard tone, as is often done in telephone engineering to measure speech transmission. The measurements require an appreciable time, and persons who suffer a large amount of fatigue will hear the tone as weaker than others will in carrying out

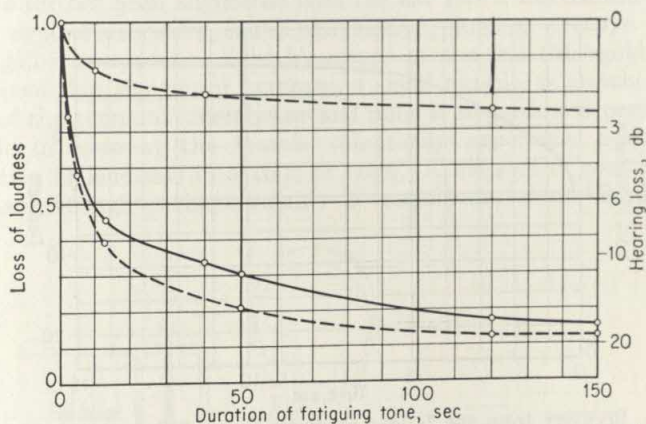


FIG. 9-44. The decline in loudness as a function of the duration of fatigue. The ordinate on the left represents relative sound pressure and the one on the right represents decibels. The tone was 800 cps at 10 dynes per sq cm.

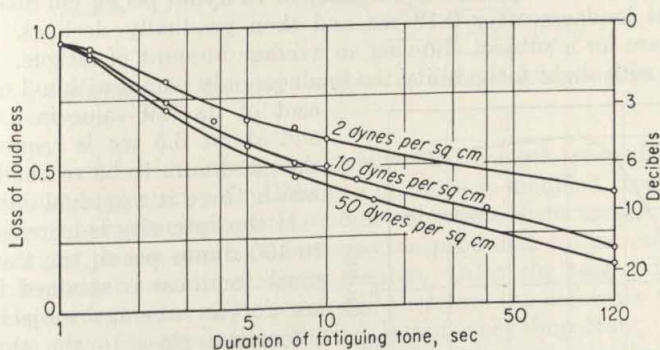


FIG. 9-45. Fatigue as a function of the intensity of the fatiguing tone. The tone was 800 cps at three intensities as indicated.

the same observations. Also, when two tones are being compared in loudness, it is often noted that the first seems louder even when the two are given exactly the same physical intensity.

To obtain an idea of the extent of recovery, one ear was stimulated for 2 min with a tone of 800 cps at an intensity of 10 dynes per sq cm. Then the tone was stopped, and after various intervals of time a tone of 0.2 sec duration and the same intensity was presented to the same ear. This brief tone was matched in loudness with another tone of equal duration

in the other ear. Figure 9-46 shows that as the interval was lengthened the tone gradually recovered its full loudness.

It is still necessary to show how the loudness of a tone develops immediately after it is introduced. For this purpose the loudness of a tone pulse of varying length was compared with that of a tone in the other ear with a constant duration of 0.2 sec. As may be seen in Fig.

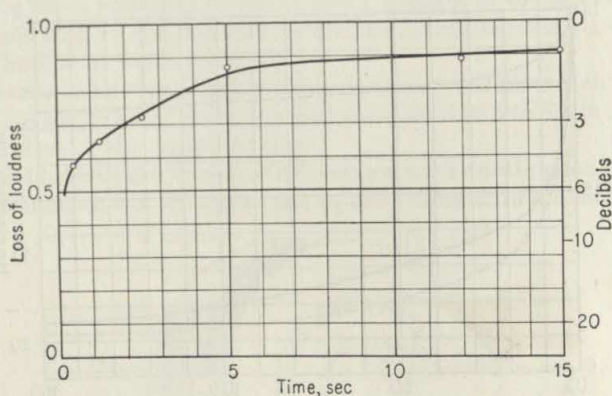


FIG. 9-46. Recovery from the fatigue produced by an 800-cps tone maintained at 10 dynes per sq cm for 2 min.

9-47, a tone of 800 cps and an intensity of 10 dynes per sq cm reaches its maximal loudness after 0.18 sec and then gradually declines. These results are for a subject showing an average amount of fatigue. For a subject with slight fatigability the loudness only comes within 3 to 5 per

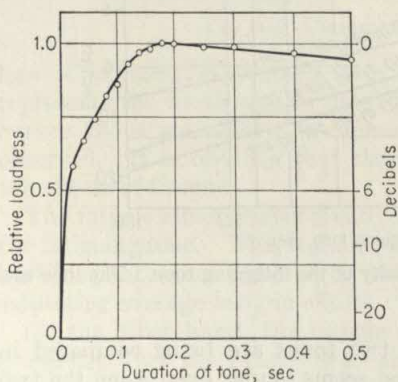


FIG. 9-47. The loudness of a tone pulse as a function of its duration.

cent of its full value in 0.18 sec, and about 0.5 sec is required for the maximum to be reached, after which there is a gradual decline.

If the intensity is increased, say to 100 dynes per sq cm, the maximum loudness is attained in 0.12 sec for an average subject. For intensities close to the threshold of hearing, however, it often happens that the attainment of full loudness occurs only after 0.5 sec.

For the frequency range studied, which extended from 300 to 2000 cps, the development of loudness followed this same course, if the tones were adjusted to the same maximum loudness. For higher tones, however, the maximum was reached usually in a 30 per cent shorter time. Yet there were large individual differences, and in certain subjects no frequency variation could be found.

Place of Origin of the Fatigue Phenomena. As already mentioned, the locus of fatigue is considered by physiologists to be the nerve endings of the basilar membrane. Here, we may suppose, the alternating pressures of the sound through an osmotic action set up changes of concentration in the various cells, and these changes produce an electrical excitation of the nerve fibers.

It has further been suggested that the ear has a mechanism for protection against excessive sound stimulation, just as the eye protects itself against too intense light by means of the iris (Mangold). It is well known that the tensor tympani, a small muscle, is attached to the center of the tympanic membrane and pulls it inward, and persons who are able to contract the muscle voluntarily experience a noticeable diminution of loudness in a tone or noise. This sort of contraction of the tensor, though perhaps smaller in magnitude, occurs involuntarily

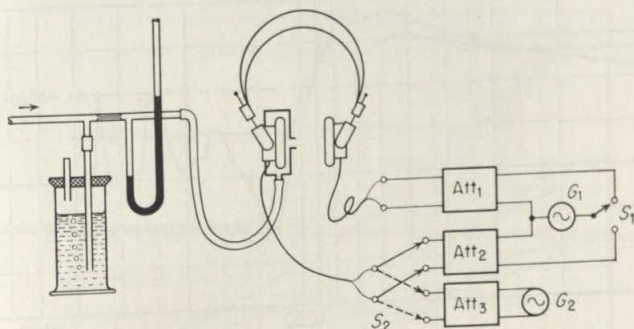


FIG. 9-48. Arrangement for studying the effects on loudness of static pressure in the external meatus.

for every acoustic stimulation and increases in strength when the stimulation becomes greater. The loudness of tones is modified accordingly. It is difficult to make a quantitative determination of the tension exerted by the tensor, but a similar effect may be produced by increasing the static air pressure in the auditory meatus. Also the tensor does not act on the eardrum at a single point, and therefore the difference between these two ways of producing tension is not very important. Kessel has already shown that such an increase in air pressure in the meatus leads to a weakening of a tuning-fork tone.

To obtain quantitative results, the arrangement shown in Fig. 9-48 was used. The case of a telephone receiver was tightly enclosed with a housing, with a connection to the meatus through a rubber tube. Another connection was made through a capillary to an air pump and a water flask, as shown. The depth of the longer tube below the surface of the water determined the air pressure, which was indicated by the manometer. For the production of negative pressures the pump was connected to the shorter tube of the flask. It is important that the changes of pressure be made slowly. Rapid changes produce a unilateral

displacement of the ossicular chain, which alters the transmission characteristics of the middle ear in an unpredictable way.

To determine the effects of pressure changes on loudness, the procedure was as follows. With the pump disconnected, attenuator b_1 was adjusted until the tones in the two receivers were equal in loudness. The pump was then started, and after a minute the attenuator was again adjusted for equality. The necessary change of attenuation represents the change in loudness. The solid line of Fig. 9-49 shows how the loudness was altered for various frequencies when the eardrum was exposed to a pressure increase of 10 cm of water. To avoid fatigue effects, these tones were presented at an intensity of 2 dynes per sq cm. As may be seen, the loudness was reduced about 6 db for all the low tones up to 1000 cps. (For other subjects this uniform range extended to 1800 cps.) This happens because the eardrum vibrates as a whole for tones below its

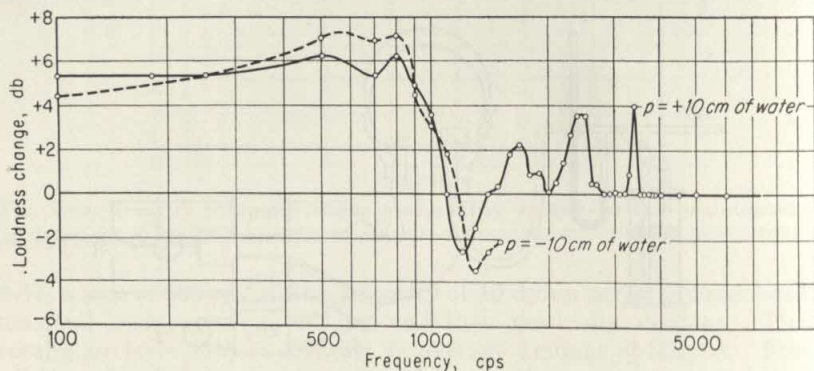


FIG. 9-49. Effects on the loudness of various tones of a static pressure of 10 cm of water introduced in the external meatus. Negative changes represent increases of loudness.

resonance frequency and an increase in its tension decreases its vibratory amplitude. As the frequency is increased, most subjects exhibit a small range in which there is an increase of loudness when the static pressure is increased. For still higher frequencies, however, only reductions of loudness occur, though in close dependence on the frequency. This relation to frequency signifies that for these high tones the eardrum is no longer vibrating as a whole, but in various independent parts, and only at certain frequencies do the ossicles take part in the movements. Kessel and Waetzmann have already pointed out this fact, which can be proved by direct observation. It may be concluded also that the minor variations shown by the auditory-threshold function in the middle range of frequencies is in part the result of segmental resonances of the eardrum.

For high frequencies, on the other hand, the changes of tension of the eardrum do not seem to have any effect upon sound transmission. This evidence thus confirms the experience of otologists that the eardrum is of no particular significance in the transmission of high tones.

If we consider more exactly the changes of loudness produced by pressure variations as shown in Fig. 9-50, it is immediately apparent

that an intense tone is weakened relatively more than a faint one. It appears that an increase of pressure converts the middle ear into a transmission system that is poorer for a strong tone than for a weak one. Hence a small static pressure makes the eardrum nonlinear in its transmission. If the eardrum is normally in the same condition of tension, then it may well be true that it is the source of combination tones, as Helmholtz suggested. In support of this position is the fact that as the static pressure increases a pure tone appears to contain an increasing amount of overtones. However, Köhler (1), by observing the movement of a small mirror cemented to the eardrum, showed that a tensor contraction produced by the loudest sounds only increases the retraction of the eardrum by about 30 per cent of its vibratory amplitude. When a sound was introduced, the light beam reflected from the mirror showed that the eardrum shifted suddenly from its resting position and then

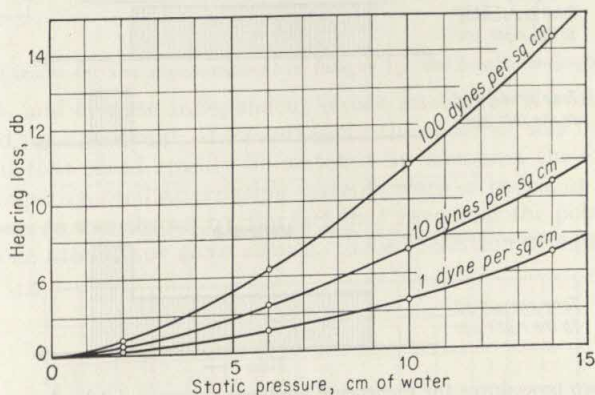


FIG. 9-50. Effects of static pressure in the meatus as a function of the intensity of the sound being measured. The results are for 800 cps at three intensities as shown.

vibrated with an amplitude that nearly reached its original position. Consequently the change of tension produced by an involuntary tensor contraction is of the same order of magnitude as the tension produced by sound pressure. For a very loud tone the sound pressure amounts to 100 dynes per sq cm or 0.1 cm of water. As may be seen in Fig. 9-50 a pressure variation of this small magnitude produces only a slight weakening of a sound, and therefore need not be considered as a factor in the production of the fatigue effects.

It is also improbable that the tension on the eardrum produced by tensor contractions can account for the magnitude of combination tones, especially when weak tones are used. Rather, these tones are mainly to be ascribed to rectification in the cochlea. It is further to be noted that a reduction of static pressure likewise causes an impairment of the loudness of the low tones, as shown by the broken line in Fig. 9-49. Hence it seems that under normal conditions the eardrum is in a state of equilibrium, even though it has the appearance of being under strong tension.

That the tension of the eardrum has no influence upon fatigue phenomena can be proved directly by comparing the fatigue curve obtained for a negative pressure of 10 cm of water with the curve obtained under normal conditions. There is no difference between these curves. Likewise the growth of loudness after the onset of a tone can have only a limited relation to tensor contractions, for an increase of static pressure of 10 cm of water only slightly affects the time of reaching the maximum: this time becomes smaller by only about 0.015 sec. Also, the tensor contraction requires a certain time to develop. Its weakening effects are still small at 0.15 sec, when the loudness maximum is attained. This effect is to be contrasted with the situation in which the eardrum is already so strongly stretched by an external pressure that a tensor contraction cannot have any further effect upon it.

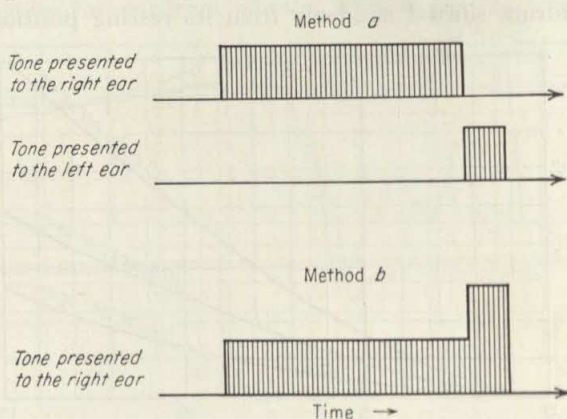


FIG. 9-51. Two procedures for measuring loudness changes: (a) loudness comparison in the two ears and (b) loudness doubling in one ear.

Finally it will be shown that the fatigue is not produced by the central nervous system. One ear can be exposed to a strong tone of long duration without any fatigue effect in the other ear.

The method used so far in obtaining fatigue functions is not suitable for present purposes. What is required is an arrangement by which the momentary loudness of a tone can be determined by increasing the sound intensity in the same ear so that the loudness seems to be doubled. In this way the fatigue of each ear can be measured independently.

The method is illustrated in Fig. 9-51. Here *a* represents schematically the temporal course of the tone presentation used earlier, and *b* represents the new method. After some practice the judgment of a doubling of loudness can be made with as much certainty as that of simple equality. This is especially true if a bracketing method is used, *i.e.*, if the loudness is changed until it is larger and then smaller than the desired value, and finally a value midway between is taken. In important cases the manipulations were made by an assistant so that the subject would not be influenced by knowledge of the situation. The two methods gave the same values for the fatigue effect.

The circuit arrangement is shown in Fig. 9-52. An oscillator was connected to three attenuators in series. Attenuator b_1 led through an interrupter to a telephone receiver that was used to fatigue one ear. After an exposure of 2 min the tone was interrupted by switch U_1 , and at the same time switch U_2 introduced the tone into another receiver. This receiver formed a part of a bridge circuit such that the currents

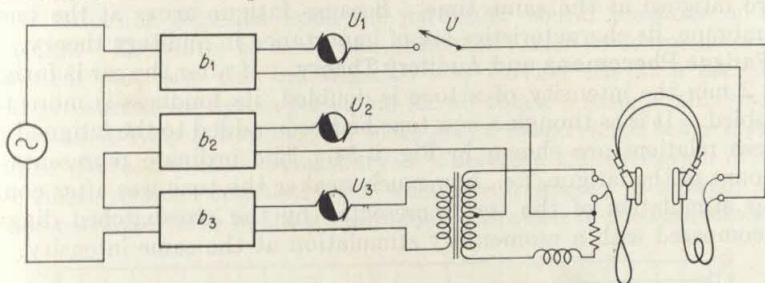


FIG. 9-52. Circuit for the measurement of fatigue by the loudness-doubling method.

through b_2 and b_3 were independent of one another. If switch U_3 also was closed for a moment, the loudness in the receiver was increased by an amount that could readily be matched by means of the attenuators. The two superimposed alternating currents were of the same size and of equal phase, as was shown by the fact that reversing the polarity of the input to one attenuator gave silence. This condition of equality could

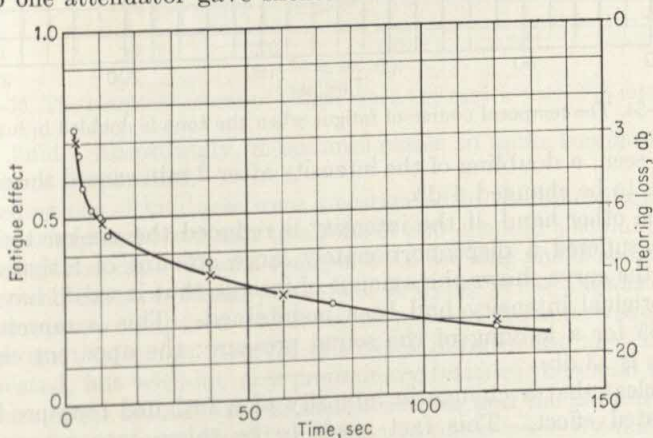


FIG. 9-53. Absence of transfer of fatigue from one ear to the other. The crosses represent measurements on one ear after the other ear is fatigued, and the circles represent measurements on the same ear when the other ear has not been fatigued.

always be attained by adjusting b_3 and perhaps also inserting a condenser across the input of b_3 , which balanced the phase error of the transformer. If the original circuit was then restored, the change in b_3 that was required to double the loudness represented the fatigue effect, for the superimposed current had to be reduced continually as time went on.

Figure 9-53 gives the results. Those represented by the crosses were

obtained after the opposite ear had been exposed for 2 min to a tone of 800 cps at 50 dynes per sq cm. Those represented by the circles were obtained without any stimulation of the opposite ear. It is clear that there is no transfer of fatigue from one ear to the other, and hence fatigue is a peripheral phenomenon.

It was further shown that the fatigue curve was unaltered if both ears were fatigued at the same time. Because fatigue arises at the basilar membrane, its characteristics are of importance in auditory theory.

Fatigue Phenomena and Auditory Theory. If after the ear is fatigued for 2 min the intensity of a tone is doubled, its loudness is more than doubled. It is as though a new tone had been added to the fatigued one. These relations are shown in Fig. 9-54. The ordinate represents the amount of the fatigue, *i.e.*, how much weaker the tone was after continuous stimulation of the sort represented by the crosshatched diagram as compared with a momentary stimulation at the same intensity. As

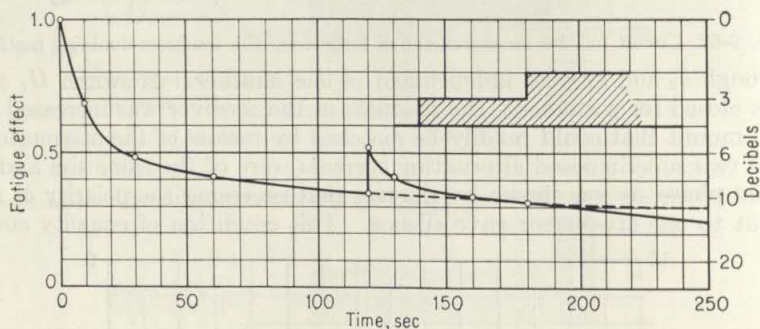


FIG. 9-54. The temporal course of fatigue when the tone is doubled in intensity.

may be seen, a doubling of the intensity after 2 min caused the apparent loudness to be changed 4 db.

On the other hand, if the intensity is reduced the weaker tone seems to have suffered a disproportionately large amount of fatigue. After a while the curve shows the amount of fatigue that it would have shown if the original intensity had been maintained. This is represented in Fig. 9-55 for a halving of the sound pressure; the apparent change in loudness is 13 db.

It is clear that a change in intensity of a fatigued tone produces an exaggerated effect. This fact needs to be taken into account in all acoustic measurements, and will be investigated further. For present purposes we may presume that when the fatigued nerve endings are exposed to a new excitation that exceeds a previous one the fatigue effect is reduced. Also, this reduction becomes greater as the second excitation exceeds the first, until finally there is no fatigue effect at all. On the other hand, if nerve endings are exposed to a smaller excitation there is an enhanced fatigue effect. When a tone has fatigued a certain region of the basilar membrane and then a tone of a different frequency is presented, this second tone must have a different pattern of action from

the usual one. Its effect is smaller in the region of the fatiguing tone than elsewhere. This departure from the usual pattern of stimulation is perceived as a noise that appears along with the usual tone. This noise is clearly audible when a sudden change of frequency is made in a long-continued tone, especially at low frequencies. Also there is a reduction in the loudness of the second tone because of the preceding fatigue.

This reduction depends upon the particular sound pressures of the two tones. Therefore, to make the principles easier to comprehend for theoretical purposes, the investigation was carried out at a constant sound pressure of 10 dynes per sq cm for all tones. Also, at this sound pressure there is equal loudness for tones over a broad range, as the equal-loudness curves indicate (Kingsbury). Therefore the excitation of the nerve fibers remains constant even when the frequency is altered, and there is constancy also in the amplitude of vibration of the eardrum and

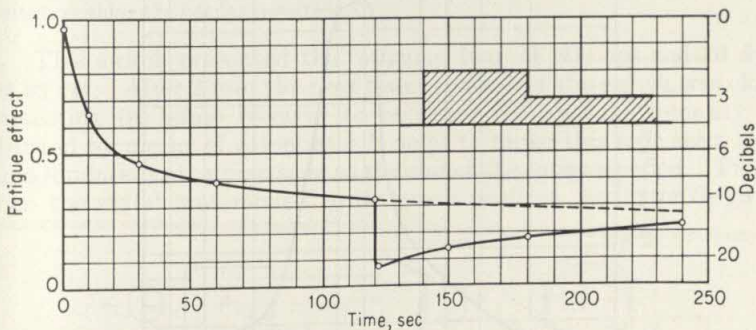


FIG. 9-55. The temporal course of fatigue when the tone is halved in intensity.

cochlear fluid. Accordingly, it becomes easier to make comparisons for two different frequencies.

The reductions of loudness were investigated in the following manner. One ear was exposed for 2 min to a tone of 800 cps and a sound pressure of 10 dynes per sq cm. Then a tone pulse 0.5 sec long and of some desired frequency and the same sound pressure of 10 dynes per sq cm was applied. This loudness was compared with a second pulse of the same frequency on the other ear. After an interval of several minutes the measurements were repeated, but without any preliminary fatigue; the sound pressure of the pulse in the second ear was kept constant, and the intensity of the pulse in the first ear was altered until the two pulses seemed equally loud. The extent to which the sound pressure of the first pulse had to be changed relative to its original value is shown in Fig. 9-56. Here we see the fatigue effect for 800 cps, and much smaller effects for frequencies above and below.

These results do not support Ewald's hypothesis, according to which the fatigue ought to be uniform for all frequencies. Moreover, the band of frequencies within which there is a mutual influence of two tones is much too broad for a resonance theory that accepts a logarithmic damping of 0.1. Nor does it appear that tones of high frequencies are fatigued

to a greater extent than those of low frequencies, as should happen according to the theories of Bonnier, ter Kuile, and Max F. Meyer.

The results lend a certain probability to the view that the nerve endings of the basilar membrane are excited by the direct pressure of fluid eddies in the cochlea rather than by the movements of the basilar membrane (see page 420). The observations of these eddies made on the cochlear model provide the best representation of the form of the fatigue function. The present view concerning the stimulation of pressure receptors is that pressure produces a change of concentration in the sensory cells by osmosis, which in turn gives an electrical excitation of the nerve fibers. On this hypothesis it is easy to understand why the rapidly alternating positive and negative pressures that constitute a tone would not produce

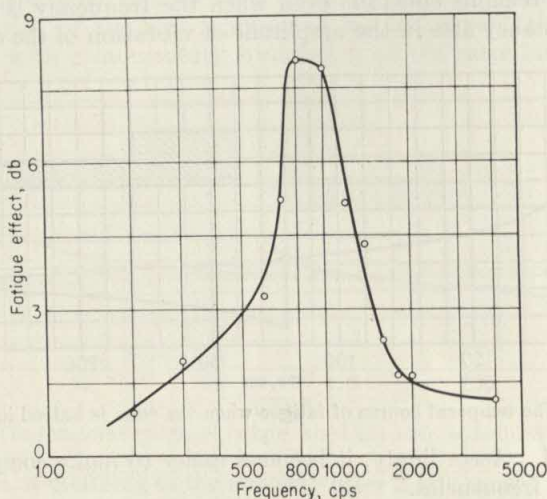


FIG. 9-56. Fatigue effects of a tone of 800 cps on various tones of equal intensity.

as large osmotic changes of concentration as are produced by the steadily acting pressure of the eddy.

It may also be shown by means of fatigue phenomena that there is a sharpening up of the pitch of a tone by operation of the law of contrast. The results are not in support of the manner of appreciation of pitch as accepted by the resonance theory, according to which every discriminable frequency sets a particular fiber into resonance and every associated nerve fiber represents only one particular tone. This follows from the fact that the pitch of a tone can clearly be altered by fatigue.

Consider, for example, the solid curve of Fig. 9-57, which schematically represents the stimulation along the basilar membrane for a tone of 800 cps. After fatigue, another tone of different frequency will have its pattern of excitation weakened on the side toward the 800-cps region, and therefore its point of maximum excitation will be shifted. The shift is downward for a lower frequency and upward for a higher frequency. Thus, in general, tones above the fatiguing tone will be raised

in pitch, and those below it will be lowered in pitch. It might also be supposed that the elasticity of the basilar membrane is reduced by fatigue, but then all tones would be raised in pitch, which cannot be observed.

To measure these phenomena, the arrangement of Fig. 9-58 was used. When the four-pole switch was moved downward from the position shown, the left receiver was first actuated through oscillator G_1 and attenuator

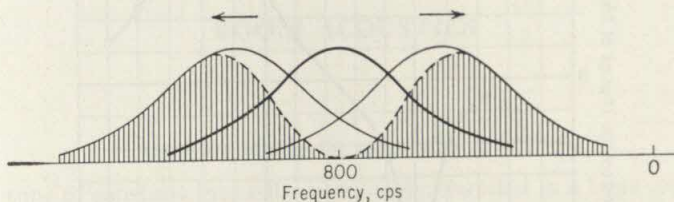


FIG. 9-57. Schema showing the effects of fatiguing with 800 cps on the pattern of excitation along the basilar membrane.

b_1 . This switch presented the fatiguing tone of 800 cps and 10 dynes per sq cm. After 2 min the next lower contact of the switch was closed, connecting the same receiver to oscillator G_2 , and the intensity was adjusted by means of attenuator b_2 so as to make this tone seem of the same loudness as the first tone at the end of the fatigue period. Finally, when the switch was moved to its lowest position, oscillator G_2 gave a

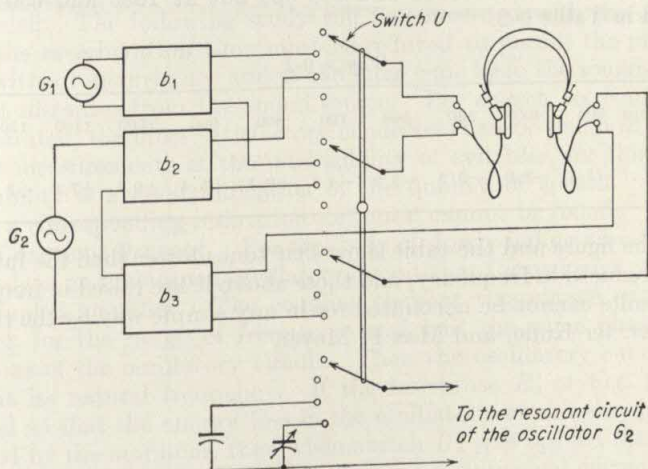


FIG. 9-58. Circuit for measuring the effects of fatigue on pitch.

tone in the unfatigued ear for a moment so that the subject could ascertain whether the pitch was the same as in the fatigued ear. The frequency of the tone in the unfatigued ear could be changed by adjusting a variable condenser in the oscillator circuit.

The magnitude of the frequency variations between the two ears after one of them had been fatigued with 800 cps is shown in Fig. 9-59. There are large individual differences, and certain persons do not show the

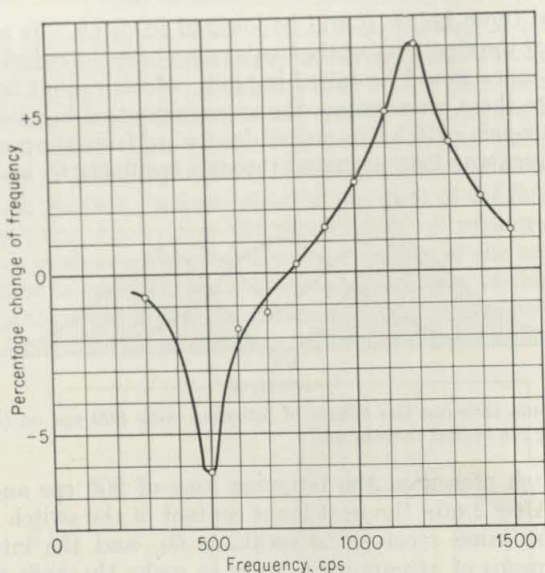


FIG. 9-59. Effects of fatigue on pitch.

maximum variations at 1200 and 500 cps but at 1050 and 650 cps as indicated in Table 9-2.

TABLE 9-2

Frequency, cps	300	400	500	600	700	800	900	1000	1100	1200	1300
Change of frequency, per cent.....	-1.4	-2.0	-3.5	-5.6	-4.6	+0.1	+5.4	+9.1	+7.8	+3.5	+1.4

Both the figure and the table show that tones lower than the fatiguing tone are reduced in frequency, and those above it are raised in frequency. These results cannot be accounted for in any simple way by the theories of Bonnier, ter Kuile, and Max F. Meyer.

CHAPTER 10

ROOM ACOUSTICS

OPTIMUM REVERBERATION TIME*

If a tone of constant intensity is suddenly sounded in a large room, the loudness attains its final value in an instant, whereas after the tone is suddenly stopped it may continue to be audible for several seconds as a sustained reverberation. The playing of music therefore is disturbed by the aftereffect produced by the room, because of the masking of the succeeding tones.

The nature of reverberation has been extensively considered in a theoretical way in recent studies by Schuster and Waetzmann, Strutt, and Eyring, and direct measurements of the reverberation time have been carried out by E. Meyer, Strutt, Olson and Kreuzer, and Wente and Bedell. The following study will be concerned with the extent to which the reverberation time must be reduced to permit the playing of music without disturbance and at the same time keep the sounds audible at great distances from the sound source. For speech, as Knudsen (3) demonstrated, the most satisfactory conditions can be found in a simple way by measurements of the intelligibility of syllables, for this form of intelligibility is a good indication of the quality of speech. Unfortunately, a corresponding indication for music cannot be found.

The Conscious Present. For the study of slowly fading vibrations, use was made of an undamped oscillatory circuit that formed part of a resistance-coupled amplifier. The coupling element was chosen so that the feedback for the range of frequency used had the same phase as the vibrations of the oscillatory circuit. Then the oscillatory circuit faded away at its natural frequency. If the resistance R_1 of Fig. 10-1 was adjusted so that the energy loss in the oscillatory circuit was just compensated by the amplifier, then when switch U_1 was opened the surge of voltage in the coil of the inductor produced a sinusoidal current of constant amplitude A . If switch U_2 was opened, the loss in the oscillatory circuit was increased and the amplitude decreased according to the formula

$$J = Ae^{-\frac{R_2}{2L}t}$$

where L is the inductance of the air-core coil and t is the time after switch U_2 was opened. When switch U_1 was closed the decay process became

* Article 9 as listed in the Author's Bibliography. Published in 1931.

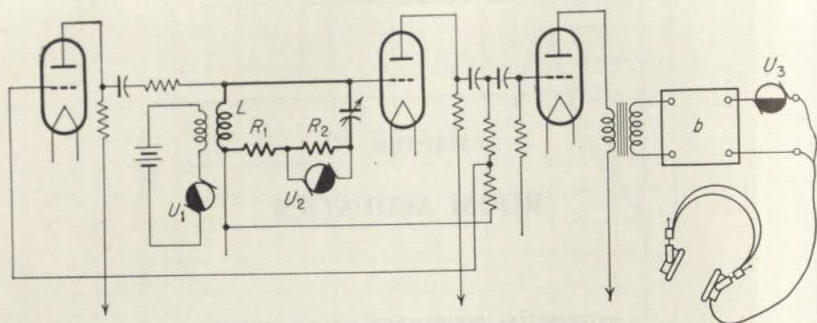


FIG. 10-1. Damped resonant circuit for the study of slowly fading vibrations.

very short because of the strong increase in damping of the oscillatory circuit by the briefly closed secondary of the coil. So that the disturbing decay process would not be audible, an interrupter U_3 was operated at the same moment to cut out the phone located beyond the attenuator b .

To a sound pressure J according to Fechner's law corresponds a loudness

$$E = k \log_e \left(1 + \frac{\Delta I}{I} \frac{J}{J_0} \right)$$

where J_0 is approximately one-fourth of the actual measured threshold, $\Delta I/I \sim 0.05$ is the difference limen for sound pressure at a high loudness level, and k is a constant.

For fading intensities the decline in loudness is given in Fig. 10-2. Though Fechner's law holds only for brief pulses of tone, the decline

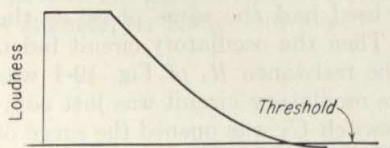


FIG. 10-2. Approximate form of the loudness function for fading tones.

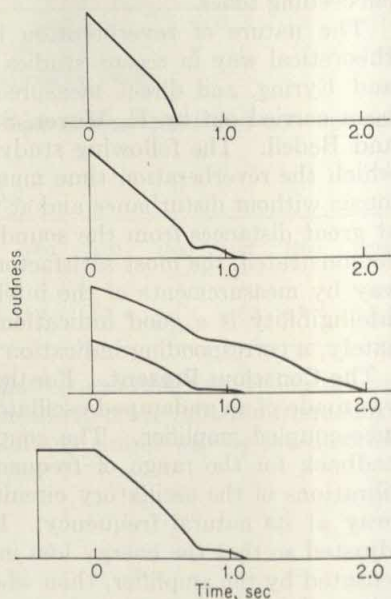


FIG. 10-3. Indicated form of the loudness function for fading tones for a number of subjects.

in loudness seems to be correctly represented, for subjectively the loudness seems to follow the course indicated in this figure. If the duration of audible fading was below 0.8 sec, all subjects represented it as a declining straight line. For longer durations, however, they drew curves like those shown in Fig. 10-3.

From these curves it is clear that after about 0.8 sec there is a slight

decrease in loudness for a period of time that is independent of the loudness of the tone. This decrease appears at a certain time after the decline of loudness begins, and a sounding of the tone for a period before the decline has no effect, as the lowermost curve of Fig. 10-3 indicates.

More exact observations showed that there actually is no momentary decline in loudness, but that it is impossible for a person to follow a continually changing phenomenon for a period longer than 0.8 sec. After this period there is a momentary lapse of consciousness, and then the loudness returns to its original level.

The sudden presentation of a weak continuous tone makes this readily observable. The constant character of its amplitude comes to consciousness only periodically. The period of time during which consciousness lapses can be reduced with practice, so that what is observed approaches more closely to the physical reality.

If the duration of the audible decline exceeds 0.8 sec the process of decline can no longer be perceived as a whole, as it is split up into parts by the momentary lapses of consciousness. The fact that unitary perception applies only to phenomena lasting no more than 0.8 sec is clearly apparent subjectively, and is well known to psychologists. Stern referred to this period of time as the conscious present.

The general significance of this period of time is apparent in the structure of speech, for the number of syllables that enter into the formation of words is such as mainly to require the conscious present for their enunciation. Only then is the word apprehended as a whole. Table 10-1 gives the percentages of occurrence of different numbers of syllables in continuous text for both nouns and verbs. It is apparent that words of more than four syllables are comparatively rare. In normal speech a syllable takes about 0.21 sec, so that in this way we obtain the value of the conscious present as 0.84 sec.

TABLE 10-1

Number of syllables.....	1	2	3	4	5	6	7
Frequency of nouns, per cent.....	17.5	45.2	22.0	11.4	3.4	0.3	0.1
Frequency of verbs, per cent.....	29.3	45.4	16.4	7.7	1.2	0.0	0.0

At the end of every conscious present a person in a sense waits for a new impression. Therefore it is clear why acoustic and visual reversals of perception appear at this periodicity. If in a long series a reversal fails to appear at the moment that it should, it is obvious that the next one does not occur at an arbitrary time, but rather after double the conscious present, so that the rhythm of the series remains undisturbed.

If the interval between the successive clicks in a uniform series is about 0.8 sec the observer has the impression, as Vierordt has pointed out, that the series is neither fast nor slow. Then each click comes at the beginning of a new conscious present, and a new click is heard always at the expected moment.

If this rhythm is beaten out with a finger, there are two impressions. One consists of the muscular movement of the finger during the conscious present, and another is the apprehension of the finger movement as a special phenomenon that initiates the conscious present. In this situation the periods are 0.1 to 0.2 sec longer. The first of these impressions is the usual one and corresponds to the conscious present for the playing of music or of listening to it.

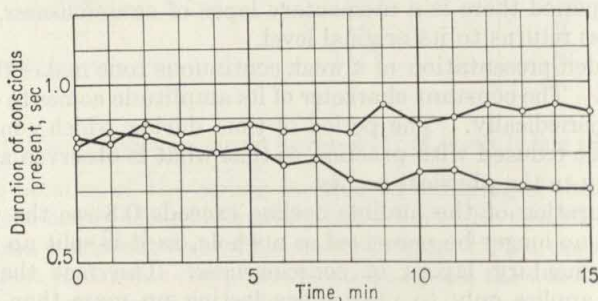


FIG. 10-4. Course of the conscious present for two different subjects.

In order to show how clearly a rhythm is perceived that seems neither fast nor slow, finger movements were recorded graphically over a period of 15 min, or more than a thousand times. Figure 10-4 shows for two subjects the mean values of the first ten movements occurring at the beginning of each minute. Thus the beating out of a rhythm that seems neither fast nor slow may be used to study the variations of the conscious present.

If another phenomenon is connected with this beating, the conscious present increases. Thus if at each beating a click is heard that is 60 db above threshold, the conscious present lengthens by 10 per cent on the average. A preliminary exposure to a continuous tone has the same effect.

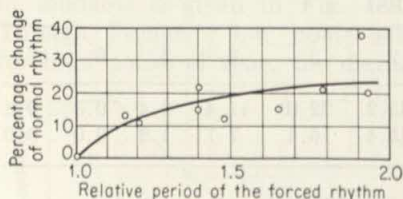


FIG. 10-5. Changes in the normal rhythm as a result of forcing another rhythm.

in as uniform a way as possible for 2 min. The mean length of the periods used are shown on the abscissa of Fig. 10-5. After a delay of 1 min the normal rhythm seemed to be prolonged to a significant degree, as the ordinate of Fig. 10-5 indicates. The points are for one subject, and the curve is the mean of a number of subjects.

If a more rapid rhythm was produced, the percentage changes were of the same order. The slow rhythm cannot be longer than twice the conscious present, for then the period is voluntarily broken into two

parts, just as a rhythm that is twice too rapid is involuntarily converted into a normal rhythm with two beats per period.

If in Fig. 10-1 the resistance R_2 is adjusted so that, as in Fig. 10-3, just three reductions of loudness (let us say) occur while the loudness is declining to threshold, these are reduced to two if just before this a slow beat is produced. This observation shows that there is an apparent reduction in the decay time. It follows that the reverberation time of a room will be heard as prolonged and as more disturbing on listening to a piece of music that is played in lively fashion, as compared with a piece played in slow rhythm.

If within the conscious present there are strong momentary variations of loudness or pitch, its duration tends to be greatly prolonged. This fact may be seen in Bolton's observation of the formation of groups in a continuous series of clicks. Thus on listening to a series of clicks in which the intervals between clicks are shorter than the conscious present, there is an involuntary assembling of several of them into a unitary temporal group, and indeed the entire series is broken up into individual groups of the same sort. Table 10-2 shows the durations of the individual groups when the number of clicks varies from two to eight.

TABLE 10-2

Number of clicks in a group	Duration of a group, sec
2	1.590
3	1.380
4	1.228
6	1.014
8	1.160

It is apparent that as the number of clicks in a group increases, the conscious present becomes shorter. This happens because as the series becomes more rapid the clicks flow together more and more and increasingly give the impression of a homogeneous stream of sound. Finally, for a continuous noise or for flowing speech the conscious present attains a value that varies little from the normal rhythm.

These preliminary studies have indicated that the rhythmic variations of loudness and pitch in music are such as to produce a conscious present lasting 1.2 sec on the average. It is still necessary to obtain a value that will be acceptable for room acoustics and other general purposes.

Individual differences in the conscious present are usually large. Various subjects have given values for a rhythm that is neither fast nor slow between 0.6 and 1.1 sec. However, the differences are much smaller for musical presentations. Good agreement was found among subjects regarding the most comfortable tempo of a piece played on a mechanical piano.

The Conscious Present and Its Relations to Reverberation Phenomena. The limited range of consciousness applies not only to temporal but also

to spatial conditions. It is possible to attend to only a relatively small portion of auditory space at any one instant, and this portion may be termed the area of apprehension. Thus if two different sounds are introduced into the auditory space at the same time, one on the right and one on the left, it is not possible to attend to the two different directions at the same time. If the eyes are closed the two sounds are heard at the same place, or else only a single sound is heard at a time and the attention jumps from one to the other, with a jump occurring at the end of every conscious present. If the two sounds have something in common, such as the same rhythm, or consist of two continuous tones of different frequency that are interrupted or weakened in the same rhythm, then these are heard at the same place. If the two tones are about equally loud and enter into the rhythm simultaneously, they seem to appear at a point midway between their true locations. If one sound is the louder or enters the rhythm earlier, the common sound image shifts in its direction.

A loudspeaker was used to produce a continuous tone of uniform intensity in an auditorium with bare walls. (The room had a volume of 250 cu meters and a Sabine reverberation time of 2 sec.) When a subject was attending to the sound, the tone was suddenly stopped. By the sudden stop the attention was focused to the sound source and the reverberation that came from all sides was put into the area of apprehension of the sound, because the sound was not stopped suddenly but gradually subsided according to the damping of the room. In this situation it was necessary to station the observer a certain distance away from the sound source so that the loudness of the reverberation was at least of the same order of magnitude as the loudness of the direct sound.

At the end of the conscious present following the cessation of the sound a new phenomenon ought to appear, and hence the area of apprehension ought to expand and the attention take on a more diffuse character. In more relaxed observations the area of apprehension was altered only after the conscious present was over, but a rapid alteration of the area of apprehension can be obtained also by a considerable effort.

If during the conscious present the reverberation did not fall all the way to the threshold, it no longer seemed to be at the locus of the sound source but seemed to be free in the expanded area of apprehension. It appeared in consciousness as spatially separate.

If the reverberation was audible only during a period that was twice the conscious present, it seemed to come always from the immediate neighborhood of the source. If it lasted still longer, the listener had the impression that it came from whatever place he directed his attention to.

To carry out these studies it was not necessary to change the damping of the room. It was sufficient to use a room that was slightly damped and to adjust the intensity of the sound so that the reverberation required the desired time to reach the threshold.

If two sounds located at different places in the room had little in common, or if the attention was especially directed to one of them, then one of these was more or less suppressed during the conscious present. This

interaction occurred also between a sound and its reverberation. There was little suppression of the reverberation produced by a sinusoidal tone because the reverberation had practically the same tonal character. Then the loudness subsided in the fashion indicated in Fig. 10-6a. For a noise, however, the reverberation has an entirely different timbre, and it is suppressed. Therefore there was a momentary decline in loudness at the switching off of the noise. The reverberation then was heard in an entirely different direction after the end of the conscious present, as the crosshatched portion of Fig. 10-6b indicates.

Many subjects were able to obtain the two different forms of loudness decline for noises merely by changing the concentration of attention. With practice, localization of sound in space was improved, the spatial attention was sometimes increased, and then the reverberation was always suppressed. The localization could be made smaller by listening with

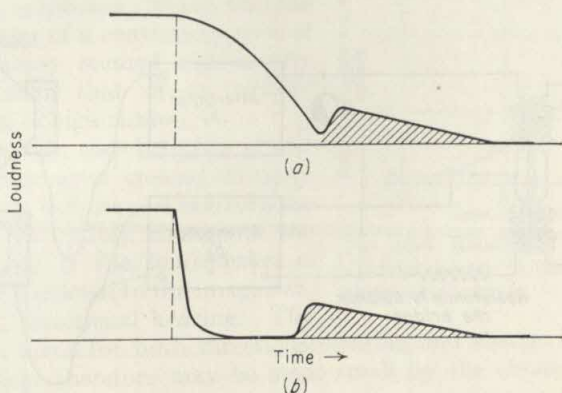


FIG. 10-6. Two forms of decline in the loudness of a sound in a reverberant room. Form (a) is characteristic of tones and form (b) of noises.

one ear. Another way was to let the tone or noise continue for 10 to 30 sec, whereupon the attention usually faded out for the loudness changes that followed. Also if the person moved about the room while making his observations, the resulting changes of direction and distance relations led to a less pronounced focusing of attention in space.

The following study shows how a spatial attitude can greatly suppress a sound. The loudspeaker L_2 in Fig. 10-7 along with its attenuator was arranged in a bridge circuit so that when switch S was opened the bridge was balanced and a sound was produced by L_1 but not by L_2 . When switch S was closed only L_2 gave a sound, and its attenuator was adjusted so that at the place of observation the two loudspeakers produced sounds that were equally loud. If the rotating switch S was set so that it was open during one half of the conscious present and closed during the other half, the subject heard a noise of constant loudness when the loudspeakers were placed close together. But if the speakers were separated by about 2 meters, a casual observation from a distance of 5 meters always gave a constant noise, whereas listening with a better

concentration of attention had the effect that only one of the speakers appeared in the area of apprehension and the loudness varied at the moment of the interruptions. During the intervals between, the second speaker came through only faintly. If the distance between the two speakers was made still greater, the loudness variations were always heard.

The fact that a sound outside the area of apprehension is either suppressed or projected into this area is responsible for the phenomenon that in a room with reflective walls not all reflections of the source are heard separately but only the sound source itself. However, in this connection it must always be noted that the loudness of a reflected image, despite the presence of large reflecting projections or surfaces, must not be greater than the loudness of the sound coming directly from the source. Otherwise the sound source will be placed in the direction of the reflecting walls. By breaking up the reflecting surfaces into numerous smaller

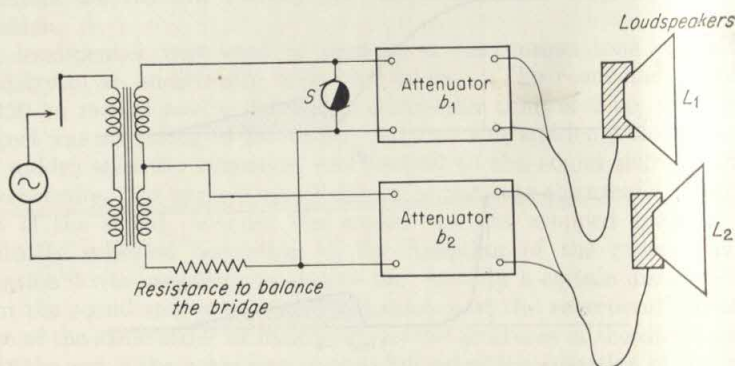


FIG. 10-7. Circuit used to study the suppression of one of two sounds according to the separation of the sound sources.

surfaces it is possible to make the various reflected patterns weak and widely distributed over the area.

The relations were entirely different if two microphones were put in the positions occupied by the two ears and these led through a pair of distortionless transmission systems to the two ears. Then the attention could be focused in a certain direction, but it was no longer possible to vary the apparent distance because it was determined by the loudness.

If only one microphone was used, there was no possibility of a determination of direction, so that in general the sound waves transmitted by the microphone were always contained within the area of apprehension. Thus the entire auditory space was always perceived at once, so that there was no suppression of the reverberation. When the source of sound was suddenly cut off the tone always faded away gradually according to the damping of the room. In this way the reverberation became much more important than in ordinary hearing. Moreover, the apparent extension of the sound source also was lost when the microphone system was used.

Apparent Extension of the Sound Source. If from a great distance one listened with closed eyes to a loudspeaker that was made to produce an interrupted tone of 800 cps at a barely audible intensity, the emitting surface of the speaker seemed to possess at most a width of a few centimeters. If the intensity was increased, however, the circular emitting surface grew larger, as shown in Fig. 10-8.

Up to a diameter of about 1.5 meters the size of the sound image was determined by the loudness at the listening point. In free space or in a reverberant room, the size of the image changed uniformly with the loudness at the listening point. If instead of the interrupted tone of 800 cps a continuous pure tone of 100 cps was used, the sound image seemed larger for the same intensities. With a shrill noise it seemed smaller. Here are the same relations found earlier in directional hearing with two earphones, where also the sound image of a continuous tone of low frequency seemed significantly broader than that of an equally loud noise of high timbre.

As the size and breadth of the sound image grew greater its edges became less definite. Therefore the smallest perceptible change in the displacement of the loudspeaker is nearly proportional to the image size, just as in directional hearing. The difference limen for both directional hearing and change in the location of the image therefore may be made small by the choice of a medium shrill noise.

The size of the sound image is independent of the breadth of the vibrating part of the loudspeaker. Two speakers of exactly the same type connected in parallel were placed at distances from each other of up to 1.5 meters without any effect on the size of the image. If the speakers were not exactly equal, however, and a difference in timbre arose, the image at this separation of the two speakers had an elliptical form when listened to from a distance of 5 meters.

If two people read the same text simultaneously it was found that the individual syllables of the sound image were exactly round. But if the texts were different and the syllables were not spoken in exact synchronism the image was broader. Finally, when there were large differences between the two speakers there was a breaking up into two separate images. Several persons are rarely able to speak or sing in a high degree of accord, and therefore the sound image of a chorus usually seems to consist of an assembly of surfaces.

For a single singer or a single instrument the connection between the changes in image size and the changes in loudness do not attract our attention. For a mixed chorus or an orchestra, however, there is a special movement caused by the waxing and waning of the sound image

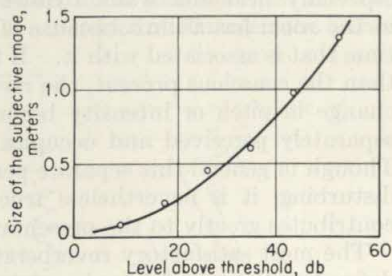


FIG. 10-8. Relation of apparent size of a sound source to its loudness at the observation point.

at different places in the group. It is likely that a certain size of image seems appropriate for every size of room, just as there is a certain size of picture that is appropriate for a given room.

Best Reverberation Time for a Concert Room. In free space the pressure of a sound declines in proportion to the distance of its source. At a great distance, therefore, the intensity is no longer adequate for musical purposes. In a room, on the other hand, repeated reflections from the walls give rise to a sound field, in addition to the direct one, whose intensity is nearly the same at all points in the room. Because of its uniform distribution this field is satisfying to all listeners. By a reduction of the absorption in the room the magnitude of the reverberation can be increased considerably in proportion to the direct field, especially near the walls. However, this improvement of audibility in the room has a limit because of the lengthening of the reverberation time that is associated with it. If the actual reverberation time is longer than the conscious present, the reverberation produced by a momentary change in pitch or intensity becomes distinct from the sound itself, is separately perceived and occupies the immediate region of the source. Though in general this separate perception of the reverberation is highly disturbing, it is nevertheless true that for a passage in fortissimo it contributes greatly to the presentation by enlarging the sound image.

The most satisfactory reverberation time for a room will therefore be defined as the actual heard reverberation time that equals the conscious present for a passage in mezzoforte. A great enlargement of the reflected sound field is therefore undesirable. The separate apprehension of the reverberation causes an involuntary concentration of attention upon the sound source, which leads to a suppression of the reverberant field, and as time goes on the concentration of attention is fatiguing.

The situation is different if the listening is done over a transmission system. Then there is no separation of the reverberation from the source. On the contrary, the apparent decay time of the instrument is usually prolonged by the reverberation, with an extremely disturbing effect. This is so because unlike ordinary listening there is no suppression of the reverberation at appropriate moments by an effort of attention. The prolonged decay time produces a jumbling of the tonal passage.

However, the optimal decay time for this case will not be considered further here, as it is mainly important for the construction of studios and for musical instruments. As the actual reverberation time depends upon the intensity of the sound source, we shall next consider how the intensity of singing or playing depends upon the size of the room.

For subjective measurements of the loudness of the free sound field in a concert room, use was made of an instrument constructed by Barkhausen and shown in Fig. 10-9. A distance from the source of about 3 meters was chosen for which the intensity of the direct sound field exceeded that of the reflected field. Then a small phone of the sort used in hearing aids was inserted into the ear, and the attenuation was adjusted while the button was pressed as shown, until the loudness of the sound presented in the small earphone was equal to that in the other

ear, which was exposed to the free sound field. Fatiguing of the ear by high intensities of sound was avoided by the use of single clicks rather than tone pulses. Also the apparatus was small enough to be kept in a pocket, so that measurements could be carried out inconspicuously. Furthermore, the great difference in the character of clicks and music made it easier to concentrate on the click by an effort of attention, because the sound in the ear exposed to the free sound field, of course, could not be switched off.

It was observed that a speaker concentrates his attention entirely on a listener, and when he is farther away he regulates his voice so that its intensity will be maintained. How well various speakers succeed in this adjustment was shown in an experiment in the open, where the speaker tried to make the intensity at various distances the same as that for normal conversation at 4 meters. Up to a distance of 40 meters the errors

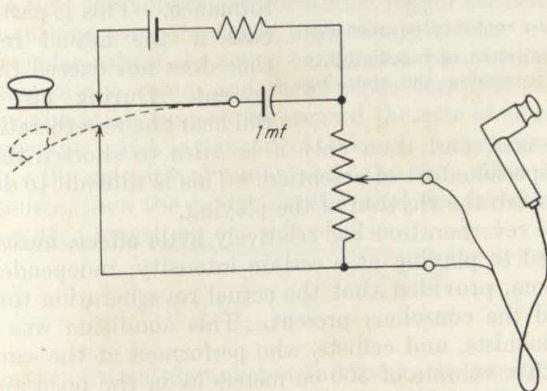


FIG. 10-9. Pocket instrument for measuring loudness.

in the adjustments of intensity were below 40 per cent. At greater distances it was not possible to speak as loudly as the conditions demanded.

These large increases in speech intensity only occur for certain vowels, like *a*, *o*, *e*. The consonants, like *g*, *m*, *n*, are spoken with little greater loudness than in ordinary speech. Therefore the quality of speech declines markedly as its intensity is increased. Figure 10-10 shows how the syllable intelligibility declines as the intensity rises above that of ordinary conversation, when measured as the percentage of syllables understood correctly on reading continuous text made up of unfamiliar syllables. The loudness was kept constant for the listener by varying the distance in the open air or by adjusting the attenuation of the transmission system. This raising of the voice is highly fatiguing, and the results showed wide variations according to the speaker's incentive and the length of the discourse.

The relations seem to be entirely different for singing and the playing of a musical instrument. Here the attention is directed so much on the performance itself that the listener is considered only incidentally. The intensity of singing is determined to a large extent by the loudness as the

singer hears it. If his threshold is raised by stopping the ears or even better by the use of a masking tone of 800 cps, the intensity of singing or playing is increased in proportion to the threshold change. However, this relation holds mainly for the faint passages. For the intense passages the intensity is limited by the maximum tension that the muscles are able to exert.

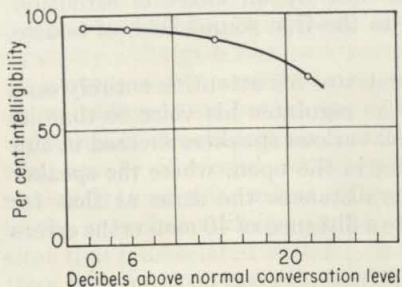


FIG. 10-10. Impairment of intelligibility as a result of increasing the speaking intensity.

the loud passages, and then only if he tries to shorten the conscious present by a special effort of attention. This is difficult to do because it is likely to disturb the rhythm of the playing.

Because the reverberation has relatively little effect, most performers are accustomed to playing at a certain intensity, independently of the size of the room, provided that the actual reverberation time does not greatly exceed the conscious present. This condition was established for singers, violinists, and cellists, who performed at the same intensity in a room with a volume of 300 cu meters as in the open air, when the distance from the listener was great.

If several persons sing the same song, as in a chorus, the radiated sound energy increases in proportion to their number. Therefore the increase in sound pressure as observed at a great distance ought to be that shown in Fig. 10-11 by the broken curve. Because the members of a chorus are spread out, however, the actual increase in loudness is relatively small. This loudness can be made to seem even less by a concentration of the attention upon a single singer. Conductors are particularly able to do this because they are practiced in singling out a particular voice. It is possible to isolate from a large mixture of sounds only something that is already known to a certain extent and which therefore has only to be recognized.

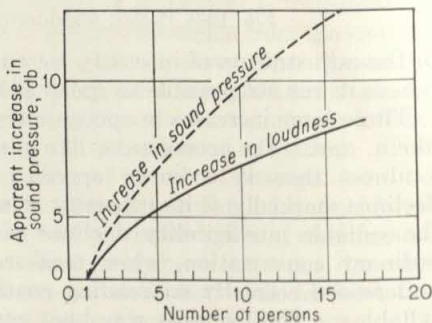


FIG. 10-11. Apparent loudness of vocal sounds as a function of the number of persons singing in a concert.

The departure of the reverberation time from its most suitable value is sensed as much more unpleasant for solo playing or singing than for the playing of an orchestra. With an orchestra the playing in accord makes the sound image large and diffuse, so that its further enlargement after the conscious present has ended does not seem strange. Also, with an orchestra, when one instrument has ceased another comes in at another place, and correspondingly the attention shifts about so that the reverberation of the first instrument is poorly observed. Therefore a long reverberation time is not as disturbing as for solo playing and singing, in which the direct sound always comes from one place and the reverberation most often comes from an entirely different place.

Hence it seems that the reverberation time should be selected so that the most satisfactory conditions are obtained for solo singers and players. Then the limited sound energy that they produce can be fully utilized. At the same time the longer reverberations for an orchestra will not be seriously disturbing even though at high energy levels.

For a particular soloist the sound energy was found to be independent of the volume of the room, and therefore in the determination of the optimum reverberation time we can regard the rate of emission of sound energy as constant. If L is this rate of emission, a the average absorption of the walls, c the velocity of sound, and t the time after the stopping of the sound source, then the energy density E of the reverberant field in a cubic space with a length on one side of D is

$$E = \frac{L}{\sqrt{3} caD^2} e^{\frac{\sqrt{3} c \log_e (1-a)}{D} t}$$

To obtain the optimal damping of the room, the energy density must reach the threshold in the conscious present $t = T_p$, or $E = H$, whereupon the relation between room size and the best damping a is given by

$$H = \frac{L}{\sqrt{3} caD^2} e^{\frac{\sqrt{3} c \log_e (1-a)}{D} T_p}$$

The reverberation time, or the time $t = T$ within which E declines 120 db, is obtained, according to Sabine, from the equation

$$T = \frac{-13.82D}{\sqrt{3} c \log_e (1-a)} \quad (10-1)$$

The following method was used to obtain the relation between the rate of radiation of sound energy in the singing or playing of a moderately loud passage and the sound energy at threshold. In a room with known dimensions D and absorption a the reverberant field was measured by means of a sound-level meter. It was necessary in these measurements to take a position as far as possible from the sound source and close to one wall, for then the direct field was small relative to the reverberant field.

If during the presentation of the sound the pressure of the reverberation is stronger than the auditory threshold by P_f/P_H -fold, then the energy density E increases with the square of the pressure, or

$$E_{t=0} = (P_f/P_H)^2 H = \frac{L}{\sqrt{3} caD^2} \quad (10-2)$$

For the measurements that were carried out, $P_f/P_H = 3 \times 10^3$, $D = 7.0$ meters, and $a = 0.14$, hence $L/H = 3.6 \times 10^{10}$.

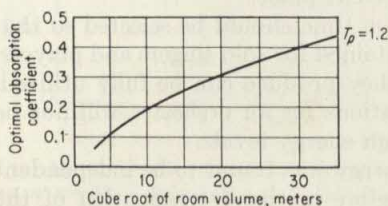


FIG. 10-12. The optimal absorption in a room as a function of its volume.

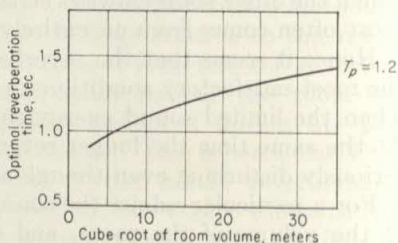


FIG. 10-13. The optimal Sabine reverberation time as a function of room volume.

The best values of a and D as calculated from these data are shown in Fig. 10-12 for a conscious present of $T = 1.2$ sec. Figure 10-13 shows the best Sabine reverberation times derived by Eq. (10-1). Finally, Fig. 10-14 shows the relation between the sound pressure of the reverberation and the threshold as dependent on room size, as calculated from Eq. (10-2).

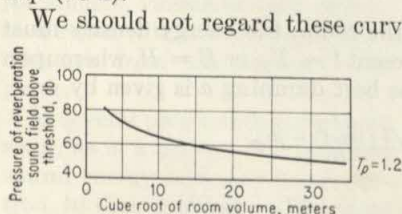


FIG. 10-14. Relation between the sound pressure of the reverberant sound field and pressure at threshold as a function of room size.

We should not regard these curves as representing the final ones, however. The actual conscious present and also the constant L/H were obtained principally from the values for classical music produced by the violin, the violoncello, the piano, and the human voice. Mean values that were reproducible to a satisfactory degree were obtained by dividing the musical presentations into strictly limited groups according to their character. Then the constants were derived for the different groups and a mean value obtained taking account of the frequency with which they occurred in the whole.

Every singer fits his program to a certain extent to the strength of his voice. Hence the value of L/H increases somewhat with room size and is not a constant. However, this correction need not apply for rooms in which D is smaller than about 10 meters. For every individual instrument, however, L/H is constant, and the mean value to be used changes only when the more powerful instruments are used in solo playing or take solo parts in the orchestra.

If the absorption α varies with frequency, two different disturbances arise. In the first place, the Sabine reverberation time varies with frequency. As in a complex clang the actual reverberation times are already different on account of their varying initial intensities, these variations in reverberation time have little effect on the timbre during the decay of the sound. In the second place, the reverberation density for a clang varies with frequency. Since the reverberation intensity at remote points in the room is greater than the direct sound, there are distortions of amplitude like those found in a filter network. The ear is highly sensitive to these distortions, and care should always be taken to make the absorption independent of frequency.

AUDIBILITY IN SMALL CONCERT HALLS*

Onset of a Sound. In rooms with slight damping it may be observed that the onset of a noise is much shorter than that of a pure tone if the reverberation time of the room is the same for both. On the basis of energy relations, which are well known (Waetzmann, 8), abrupt switching on and off of a steady sound source gives a rise and fall of the sound energy density E of the room according to the equations

$$E = E_0(1 - e^{-kt}) \quad \text{and} \quad E = E_0e^{-kt}$$

when t is the time and k is a constant. The two curves when added give a constant result. For sound pressure, which varies as the square root of the energy density, this is not true because the square-root relation doubles the decay time, while the onset is considerably shortened. This shortening of the onset relative to the decay appears in part *a* of Fig. 10-15, which represents an oscillographic trace of the sound pressure of a 1000-cps tone warbling by ± 10 per cent at a rate of twenty times per second. However, this shortening of the onset process is only obtained with warbles with large frequency variations and with irregular clicks and noises. Even a reduction of the frequency modulation of the above tone to ± 2.5 per cent gives an onset that is little different from the decay, as part *b* of Fig. 10-15 shows. In this situation the transient equation as derived on the basis of energy relations no longer holds because phase relations have been neglected, as has already been proved by Strutt (5).

As part *c* of Fig. 10-15 shows, the onset and decay times are exactly the same for a pure tone. If as in this instance the microphone is placed in a corner of the room, where walls and floor are mutually perpendicular, then with the microphone at a pressure node a nearly exponential onset and decay of sound pressure is obtained if the frequency used is a natural frequency of the room (Knudsen, 4). Especially if the damping of the room is small, its resonance is so sharp that the vibratory amplitude of the resonant tone greatly exceeds the amplitude of other adjacent natural frequencies set up by the transient. Therefore the whole room behaves like a system with one degree of freedom. If the microphone is not located in a pressure node of the vibration existing at the end of the

* Article 16 as listed in the Author's Bibliography. Published in 1934.

transient, or if the exciting frequency is not in agreement with the natural frequency of the room, then the transient vibrations of the neighboring natural frequencies may become greater. Because these are the same for starting and stopping the sound source, it follows that the changes of sound pressure arising at starting and stopping are exactly the same to the finest detail over a long period of time, as parts *d* and *e* of Fig. 10-15 illustrate.

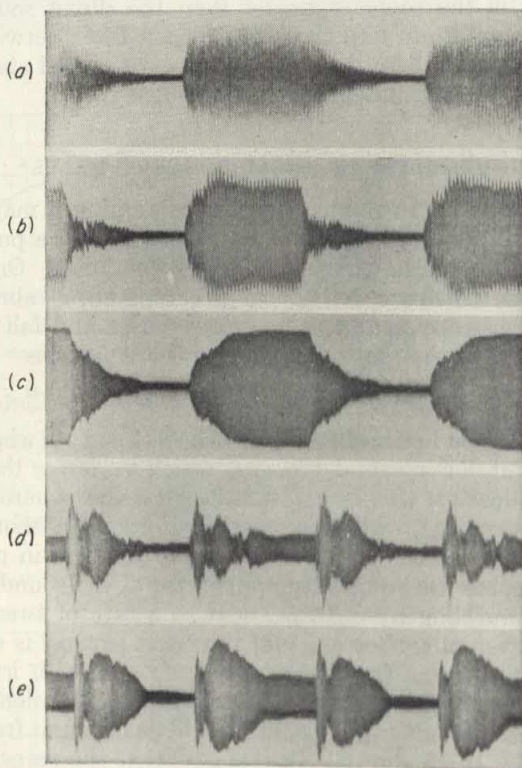


FIG. 10-15. Oscillograms of various kinds of sound pulses in a reverberant room. The room had a volume of 180 cu meters, and the sound pulses lasted 1.6 sec. (a) Warble tone, modulated ± 10 per cent; (b) warble tone, modulated ± 2.5 per cent; (c) pure tone; (d) and (e) pure tones not tuned to a natural frequency of the room.

If the tone does not appear or disappear suddenly, but has a certain time of rise and fall as in most musical instruments, the amplitude spectrum of the tone pulse becomes narrower. Then only those natural frequencies of the room that are closely similar to the exciting tone are involved. Because their frequency differences are small, the beats are extremely slow, and the onset and decay curves are smoothed out. The lower portion of Fig. 10-16 is an oscillogram of a tone that was switched on and off by means of the circuit of Fig. 4-29. The upper portion of this figure shows the transients obtained in a room with a reverberation time of 3.0 sec when the sound source was switched on suddenly and the

middle portion shows the transients of the room when the sound source was switched on gradually corresponding to a reverberation time of 0.2 sec. Because these two curves show a closely similar form it appears that the large departures from an exponential form of decay that often are found are largely due to the beating of adjacent natural frequencies.

The following tests were made to clarify this situation. In a room with a volume of 180 cu meters the reverberation time T was given different values of 3.4, 1.8, and 0.65 sec, and series of tone pulses of 1600 cps and durations Δt of 0.04 and 0.32 sec were presented. The pulses were

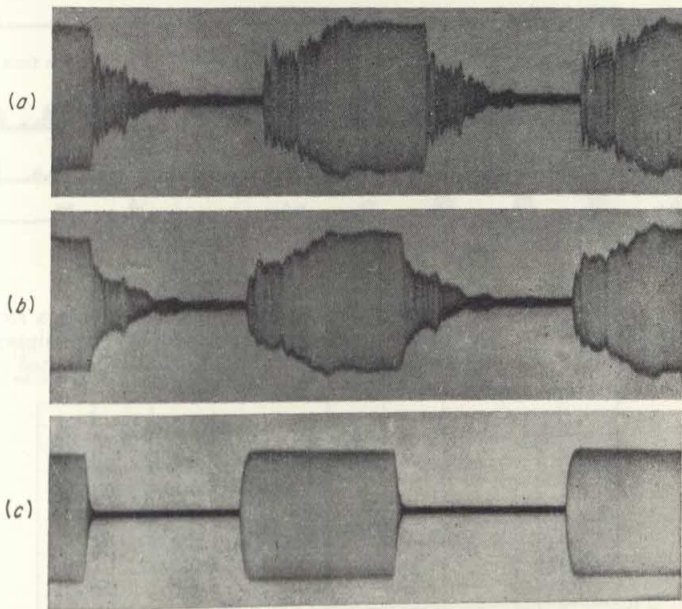


FIG. 10-16. The reverberation curves become smoothed if the switching is gradual. (a) is for a room with a reverberation time of 3 sec and sudden switching, (b) is for the same room, but with a gradual on and off switching corresponding to a reverberation time of 0.2 sec, and (c) is the onset and decay of the sound source.

recorded at ten different points in the room, with results as indicated in Fig. 10-17. It is evident that the rise of sound pressure was changed but little with the reverberation time, especially in comparison with the decay processes. It is further shown that there was little effect of the reverberation time on the sound-pressure relation between pulses of 0.04 and 0.32 sec duration.

This rise in the sound pressure at the onset of the tone is greatly shortened as compared with an exponential form of rise, and this condition is responsible for the following observation in the room referred to above when it was given a reverberation time T of 3.5 sec. A series of tones was presented at regular intervals beginning with 1000 cps and increasing by half-tone steps until 2000 cps was reached, when the series was ended. Even though the individual tones lasted only 0.03 sec it was still possible

to observe the steplike increase in pitch. Only when the intervals were further decreased did the experience change into a continuous glide of pitch. A reduction of the reverberation time of the room to 0.65 sec had no noticeable effect on the interval at which the change to a glide appeared. The same results were obtained for a room with a volume of

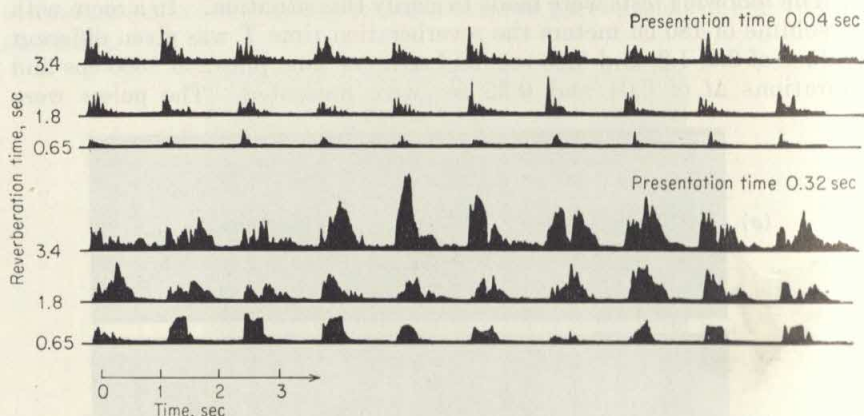


FIG. 10-17. Oscillograms of tone pulses as recorded at ten locations in a room that was given three different reverberation times as indicated. For the upper set of measurements the pulses lasted 0.04 sec, and for the lower set they lasted 0.32 sec.

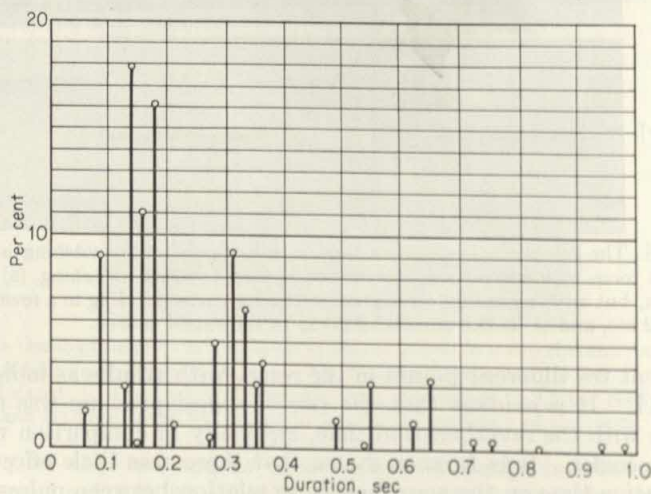


FIG. 10-18. Distribution of the durations of tones in violin playing. The music was the first violin part of Beethoven's Fifth Symphony.

2000 cu meters and a T of 2.0 sec. Figures 10-18 and 10-19 show that the most frequently occurring durations and intervals in music are considerably longer than this.

Relations of Reverberation Time to Frequency. Many observations show that the tents used by shows and circuses often have astonishingly good acoustics, far better than usually found in wood-paneled rooms.

It was generally assumed that covering walls with wood had a favorable effect because of the great velocity of sound in the panels. Yet at the outset it was clear that the good acoustics of the tent were due merely to the fact that the movement of the fabric produced a great absorption of low frequencies as compared with high frequencies. Also E. Meyer and Cremer have shown that the beneficial effects of a wood lining are due to certain favorable frequency relations of the reverberation time (see Wentz; MacNair; Knudsen, 5; Strutt, 1).

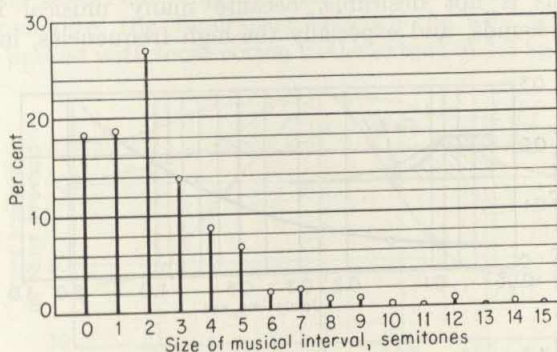


FIG. 10-19. Distribution of musical intervals in violin playing. The music was the same as in the preceding figure.

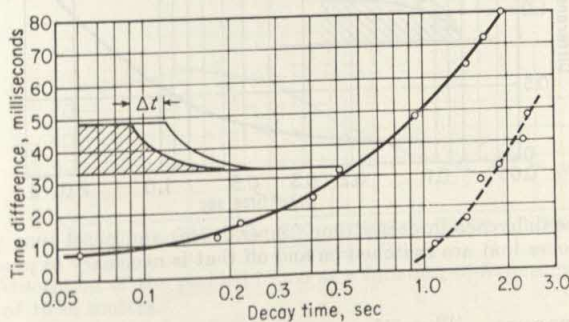


FIG. 10-20. Time differences necessary to produce timbre changes when two tones are switched on and off, as a function of their decay times.

The significance of frequency in relation to the reverberation time was shown by the fact that when two tones of 1000 and 400 cps and loudness levels of 60 db were switched on and off there was a noticeable change of timbre if the two tones were not synchronized, but in the switching there were time differences between the two of 2×10^{-3} sec. The order of the tones in the series was unimportant. If the two tones had the same decay time T , as shown on the abscissa of Fig. 10-20, it was necessary to have a time difference as indicated on the ordinate in order to obtain a change in timbre as compared with the synchronous condition. The broken curve gives similar results for the onset of the tones.

The ordinate of Fig. 10-21 shows how much the decay time T of one

of the two tones had to be changed, starting from a synchronous relation for onset and decay, in order for a change of timbre to occur in comparison with the situation in which the two tones had the same onset and decay times. These changes in the transients are greater than those necessary for a perceptible change in the transients of a single tone (see page 325). The difference limen for the first case is one of timbre, whereas for the second it is one of time.

The heavy damping of the high frequencies that is often found in concert rooms is not desirable, because many musical instruments radiate their sounds, and especially the high frequencies, in a strongly

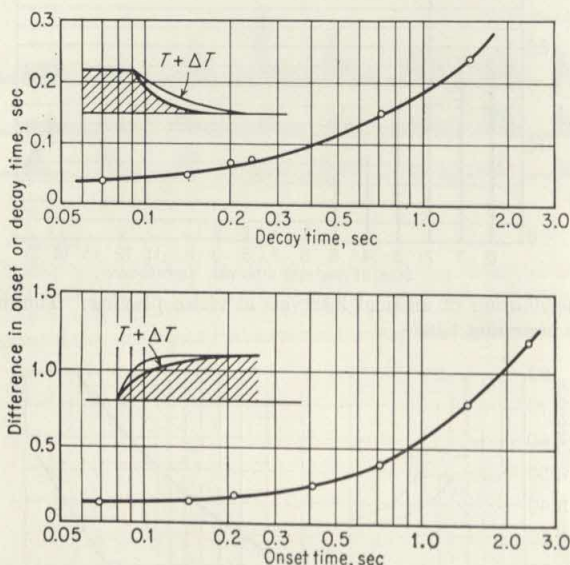


FIG. 10-21. The difference in decay time (upper curve) and onset time (lower curve) between two tones that are switched on and off that is necessary to produce a difference in timbre.

directional manner. Thus the sound energy is not distributed throughout the room to a sufficient extent by repeated reflection from the walls. Some relevant measurements are given in Fig. 10-22. Here the curve marked $T = 0$ represents the directional radiation of a loudspeaker in the open air emitting a warble tone of 2000 cps. The ordinate indicates the variations of sound pressure produced by rotating the speaker about its center line. The two upper curves show the changes of sound pressure produced by the same rotation when observed in a room with a volume of 100 cu meters and reverberation times of 1.0 and 1.6 sec.

The loudness changes produced in ordinary hearing by changing the orientation of the loudspeaker are greater than the changes in sound pressure recorded with a microphone, because the concentration on the loudspeaker gives a certain degree of suppression of the reverberant field. The difference varies between 2 and 7 db.

To investigate the effects on the acoustic quality of a room of the relations of the reverberation time to frequency, an arrangement of absorbing material was used to give effects similar to those in a tent. It consisted of a wooden frame 2 meters wide and 4 meters long divided lengthwise, with wire netting on one side and 1- by 4-meter pieces of canvas on the other side, which was the side exposed to the sound. The canvas had a weight of 350 grams per sq meter and was coated so that for the most part it moved like a diaphragm under the action of sound waves. As a result it was highly absorbent, especially for the low tones. To avoid any points of resonance, the 4-cm space between the wire netting and the canvas was packed with loose cotton to the extent of 1.3 kg per sq meter.

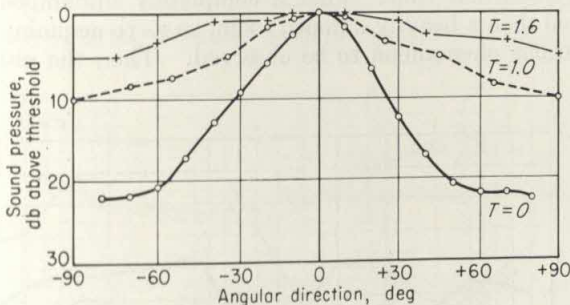


FIG. 10-22. Effect of reverberation on the directionality of the sound radiation of a loudspeaker.

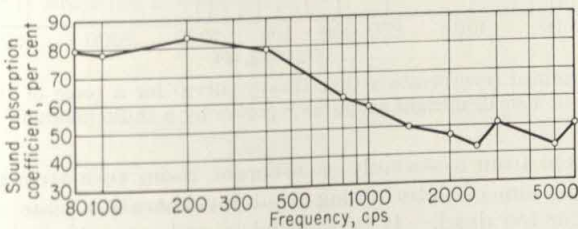


FIG. 10-23. Absorption of the padded frame as a function of frequency. The sample had an area of 16 sq meters.

The variation of the absorption with frequency, as measured by the reverberation method, is shown in Fig. 10-23. By making the coating of the canvas stiffer it is possible to reduce further the absorption of the high frequencies as compared with the low frequencies. However, the results shown in Fig. 10-23 seemed satisfactory. All the materials were fireproofed. If the frame was turned around so that the sound first struck the cotton layer, the absorption was increased for the high frequencies without any change occurring for the low frequencies. The frame therefore served as a convenient means of altering the reverberation time in its relations to frequency.

Optimal Reverberation Time. A determination of the optimal reverberation time was made in a manner similar to that already used by Sabine and Lifshitz, by placing a varying amount of absorbing material

in a room, with equal distribution on the walls and ceiling. Used for this purpose were several hundred square meters of the padded frames described above, as well as simple wooden frames containing cotton held between wire nettings. These frames when placed at the proper distance from a wall will give an absorption that increases regularly with frequency. Also used was a thin velvet material that had an appreciable absorption only for frequencies above 1000 cps when placed directly on the walls or floor. The subjects used in the tests were music teachers, music lovers, radio amateurs, and a number of famous artists and members of the musical academy. To prevent the subjects from influencing one another, each one separately made the judgments of optimal reverberation time. First a completely undamped room was presented and then a heavily damped room, so as to acquaint the subject with the various phenomena to be observed. Then the procedure was

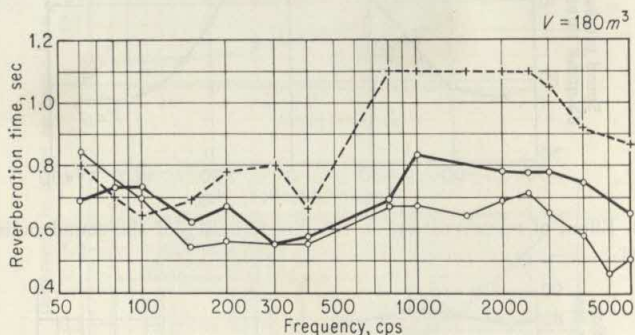


Fig. 10-24. Optimal reverberation time (heavy curve) for a room of 180 cu meters for the music of a small upright piano, as reported by a radio amateur.

to go by steps from a strongly reverberant room to a strongly damped one, with the aim of determining what reverberation time was neither too lively nor too dead. It is essential in order to obtain reproducible results to approach the best value stepwise from both sides. The most satisfactory frequency relations were determined at the same time, by alternating the brightest timbre with the dullest until the best conditions were found. No large variations among the various subjects could be found. The artists differed from the unmusical persons only in being more clear and definite.

Sample results are given in Figs. 10-24 and 10-25 for a room with a volume of 180 cu meters. Here the solid line represents the best reverberation times for the music of a small upright piano as reported by a radio amateur and an expert on musical esthetics. The broken line represents a condition that was judged as too reverberant and too shrill, whereas the thin line represents one that was too dull and too quickly damped. Figure 10-26 gives values obtained by a noted conductor for music of a grand piano in a room of 400 cu meters. Figures 10-27 and 10-28 show the

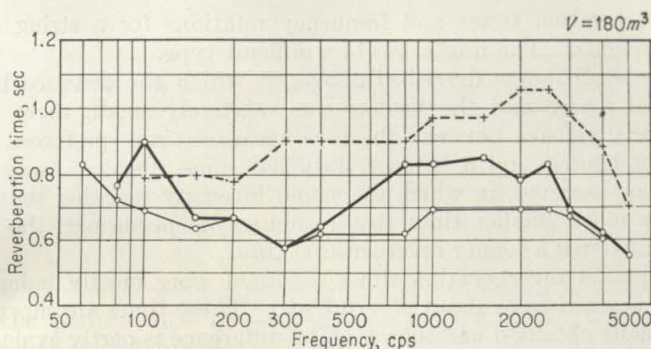


FIG. 10-25. Same as in the preceding figure, as reported by an expert on musical esthetics.

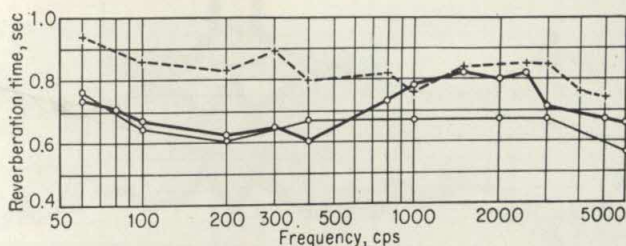


FIG. 10-26. Optimal reverberation time for a room of 400 cu meters for the music of a grand piano, as judged by a noted conductor.

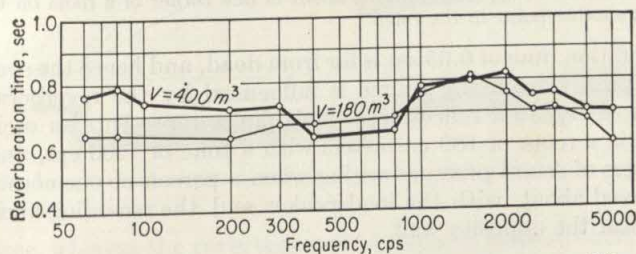


FIG. 10-27. Optimal reverberation times for a string quartet in two different rooms.

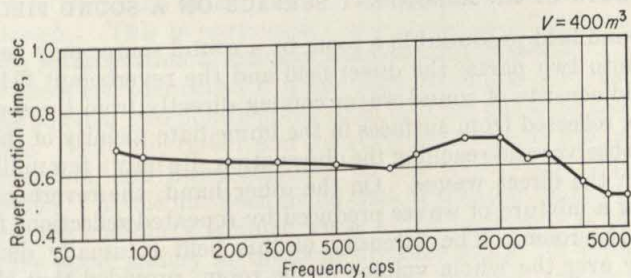


FIG. 10-28. Optimal reverberation times for singing in a room of 400 cu meters.

best reverberation times and frequency relations for a string quartet and for singing. The music was of a difficult type.

In the small rooms described above, in which the distance between the sound source and the listener was relatively small, there was no particular difference between the reverberation times preferred by the performer himself and a listener stationed some distance away. In a large room, however, in which the sound intensity reaching the listener might be much smaller than that reaching the performer, the distant listener preferred a longer reverberation time.

The optimal reverberation times obtained were mostly independent of frequency and were about $T = 0.7$ sec. These times are shorter than those usually obtained heretofore. The difference is partly explained by the fact that most of the values that have been reported were calculated and not directly measured. Figure 10-29 shows that even a room with

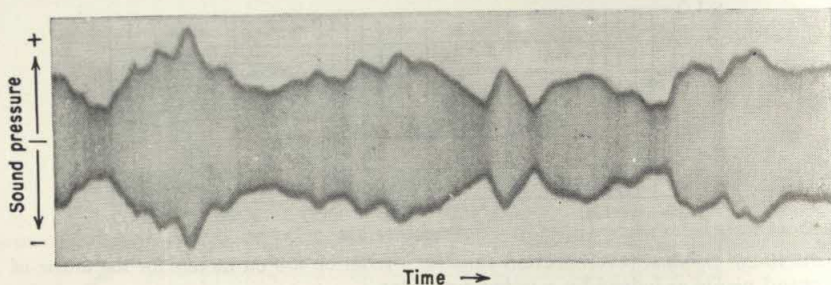


FIG. 10-29. Effects of a person moving about in one corner of a room on the sound pattern at another point in the room.

a reverberation time of 0.65 sec is far from dead, and hence the sound field coming directly from the source is influenced by the reverberant field arising from repeated reflections. This figure represents an oscillogram obtained in a room of 180 cu meters with a tone of 1600 cps, and shows the changes of sound pressure arising when a person in one corner of the room moved about, with the loudspeaker and the recording microphone located near the opposite wall.

EFFECTS OF AN ABSORBENT SURFACE ON A SOUND FIELD*

The sound field produced in a room by a sound source may be divided roughly into two parts, the direct field and the reverberant field. The direct field consists of sound waves coming directly from the source and also those reflected from surfaces in the immediate vicinity of the source or of the observer and reaching the observation site only a few milliseconds later than the direct waves. On the other hand, the reverberant field consists of a mixture of waves produced by repeated reflections from the walls of the room. The intensity of this field is usually distributed uniformly over the whole volume of the room, provided that the room does not contain any focusing surfaces.

* Article 13 as listed in the Author's Bibliography. Published in 1933.

Early in the development of the science of architectural acoustics it was believed that the listening quality of a room was determined by the direct field. More recently, however, a greater significance has been ascribed to the reverberant field, and special rules have been worked out for the most suitable onset and decay times.

According to the work of Backhaus (3), the onset and decay times for speech, singing, and musical instruments are of the order of 0.05 sec. Thus they are small relative to the reverberation times of rooms. It is therefore clear that the initiation of sounds, or the "attack," as it is called in phonetics, which is the main feature in singing and playing that gives the performance its individual character (Trautwein), becomes obscured in the reverberant field by repeated reflection from the remote surfaces of the room. The direct sound field falls off with distance from

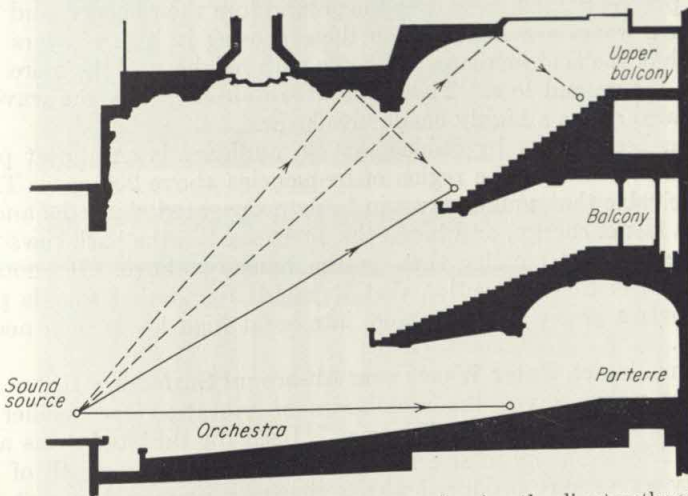


FIG. 10-30. Longitudinal section through a theater showing the direct paths of sound from the stage.

the source, whereas the reverberant field remains constant over the area, and so with increasing distance from the source the direct field becomes smaller relative to the other, and at the same time the peculiarity of the attack lessens. This is particularly true in the back parts of the room where the reverberation is stronger than the direct sound.

From these considerations it would seem to follow that the audibility should be equal at two points in the room that are the same distance from the source. Both the direct and the reverberant fields will be the same at these points, and other relations do not seem to be important for intelligibility. Yet it has been found that in theaters and concert rooms in general the audibility is much worse in the back rows of the parterre than in the upper gallery at the same distance away. It is not that the sounds in the parterre are not loud enough but that the details of the playing cannot be heard.

Figure 10-30 represents a cross section through a theater, showing that

the back rows of the parterre are reached mainly by sound waves that pass over the heads of the listeners seated in the orchestra. On the other hand, the early rows of the upper balcony are reached by many waves going directly from the stage and by others that have undergone a single reflection from the ceiling and strike the ears of the audience from above. The ceiling of the first balcony reflects hardly any waves to the parterre, because for architectural reasons it is on a line with the waves coming from the stage.

Weakening of Electromagnetic Waves by an Absorbing Surface. It is well known in wireless telegraphy (Strutt, 2, 3, 6, 8) that when electromagnetic waves are propagated along the poorly conductive surface of the earth the waves are greatly attenuated. There is a continuous loss in the energy of the electromagnetic field in the poor conductor. The waves passing immediately over the ground lose their energy, and therefore these waves are weaker than those passing in higher layers. The strength of the field increases markedly with height, and the more so the greater the ground loss. These effects are absent when the waves are propagated above a highly conductive layer.

It has been shown by Sabine that an audience is an almost perfect absorber of sound in the region of frequencies above 200 cps. Thus it is conceivable that sound waves in being propagated along the audience suffer a loss of energy, and hence the direct field in the back rows of the parterre becomes smaller than in the balcony above. It should be mentioned in this connection that Reynolds found that sounds propagated over a grassy field are more intense at high levels than near the surface.

Attenuation of Water Waves near Absorbent Surfaces. It was found that for water waves the amplitudes of vibration are smaller near absorbing surfaces than farther away. Used for this study was a level trough 2 by 2 meters in size and filled with water to a depth of 2 cm. Gravity waves were produced with a vibratory plunger driven at 5 cps. The floor of the trough was finished in matte black and the water was colored black, so that there were reflections only from the fluid surface. If a point source of light was placed about 1 meter above the water and its image was observed in the water surface, it was seen as a line because of the wave motion of the surface. This line had a direction corresponding to the direction of propagation of the waves, and its length was a measure of their amplitude. These lines of light could easily be photographed. By placing the lamp in different positions it was possible to measure the whole expanse of the wave field. The wavelength could best be determined with standing waves.

To study the whole pattern of wave motion of the water surface a rectangular frame was used on which iron wires were stretched parallel to one another and then heated until they glowed with a yellow color. This frame was placed near the water surface with its longer dimension perpendicular to the direction of propagation of the waves, and the reflections of light from the water surface were observed. When the wave field was quite uniform a series of parallel lines of light was seen,

and the width of the lines diminished with distance from the disturbed surface. In the picture (Fig. 10-31) the location of the vibrating plunger is indicated by a white spot. Then if a long strip of water-soaked cotton was placed in the trough it produced a region of high absorption. The water in its neighborhood did not vibrate at all, and only at some distance corresponding to several wavelengths was the original amplitude attained. Here it was necessary that the vibrating plunger be about one wavelength from the cotton. The lower portion of Fig. 10-31 shows how the damped effect is extended when the wavelength is increased.

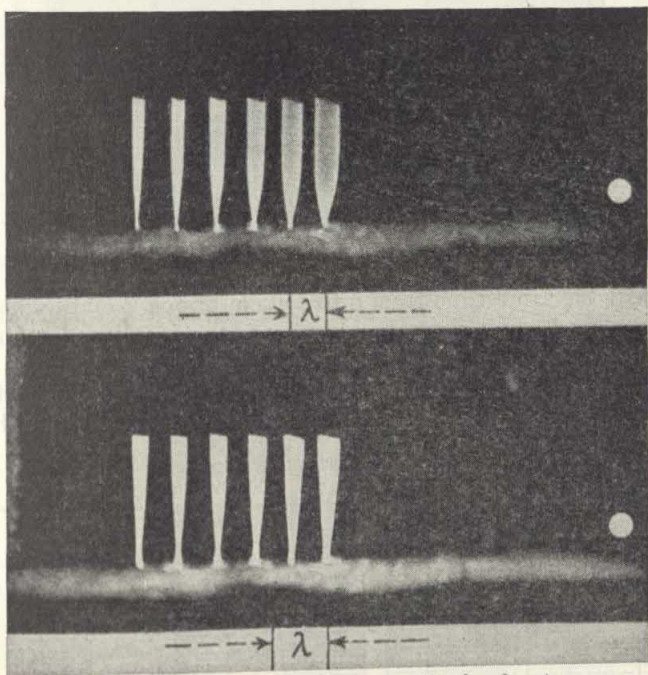


FIG. 10-31. Effect of an absorbing layer on the amplitude of water waves, shown for two different wavelengths. The wave is progressing from right to left.

Attenuation and Distortion of Sound Waves during Propagation along an Absorbent Surface. To study the magnitudes of these effects with sound waves also, a frame was constructed as shown in Fig. 10-32, with dimensions of 2 by 12 meters, and placed horizontally in the open air at a level of 1 meter or more above the surface of the ground. The frame contained thin wires spaced at 20 cm distance, and was covered with a layer of cotton held on by threads. A loudspeaker was placed at one end of the frame, and the sound measurements were carried out at a point 12 meters distant from the other end. The loudspeaker had a diameter of 20 cm, and its direction of radiation was carefully adjusted so that in the immediate vicinity of the measuring instrument there was a homogeneous field when the absorption layer was absent. Control measurements were carried out with small loudspeaker diaphragms also.

Figure 10-33 gives results for a tone of 800 cps and for a location of the loudspeaker 30 cm above the absorbing layer. The figure shows the changes of sound pressure, relative to the undistorted field, when the length L of the absorbing layer was increased by successive steps up to 12 meters and the height at which the measurements were made was

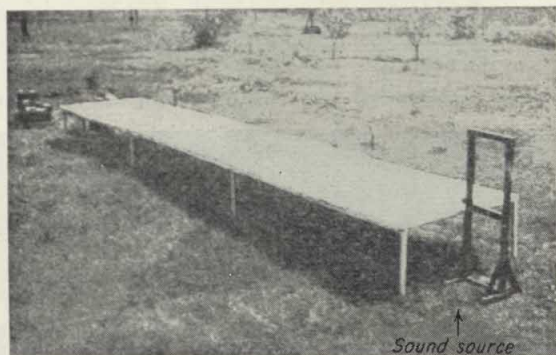


FIG. 10-32. Frame for the study of sound propagation along an absorbing surface.

increased at the same time from 5 to 150 cm above the absorbing layer. It is surprising to find that the absorbing layer produced a noticeable effect at very great distances.

Figure 10-34 shows how the modifications of the sound field varied with the level of the loudspeaker for a tone of 800 cps and an absorbing

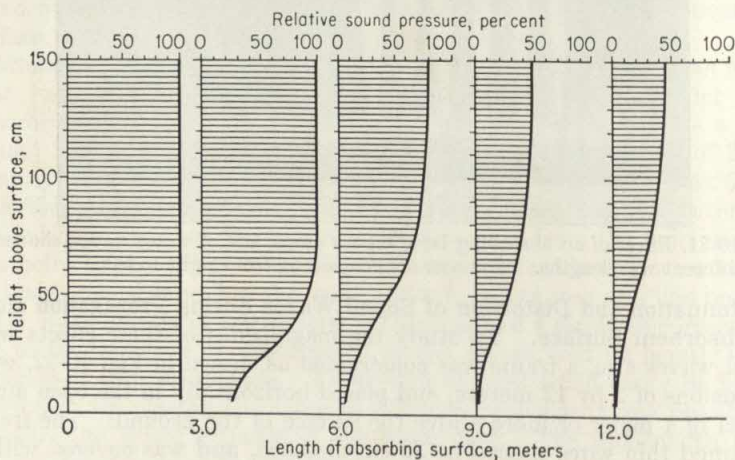


FIG. 10-33. Effects of length of the absorbing surface and the distance above it.

surface 12 meters long. The final curve on the right shows that there was no longer any effect on the original sound intensity when the speaker and the point of measurement were more than 1.5 meters above the absorbing surfaces.

There is a strong absorbing effect of grass, and measurements of this

kind made on such a place as a lawn would have to be carried out at least 1.5 meters above the ground to avoid any disturbance from the surface. The study of water waves indicated that the level of influence increases as the frequencies are made lower. Therefore if frequencies below 800 cps were used, these heights above the ground would have to

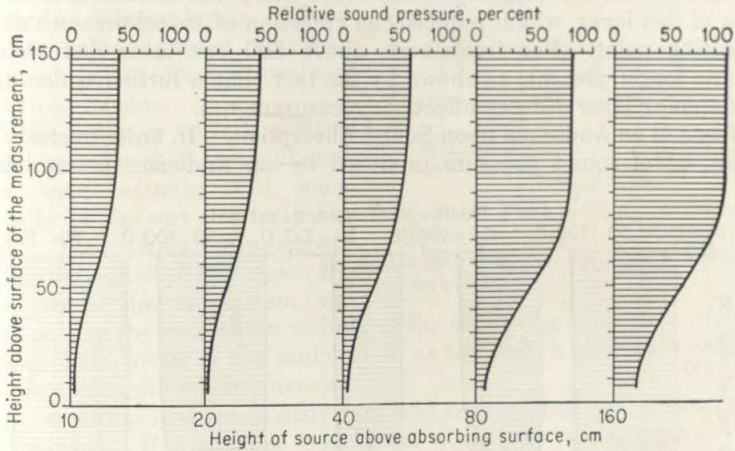


FIG. 10-34. Effects of the position of the sound source above the absorbing surface.

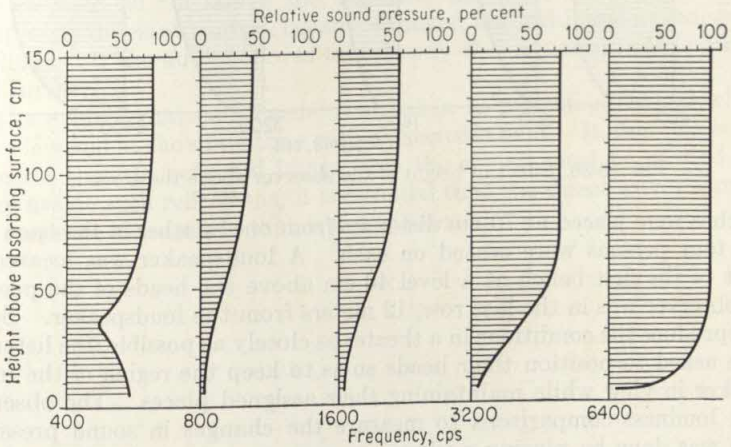


FIG. 10-35. Effects of height above the absorbing surface for various frequencies.

be enlarged. They would have to be enlarged also if the distance between the sound source and the point of measurement were made greater.

Disturbances in Relation to Frequency. The changes in the sound field are shown in Fig. 10-35 as a function of frequency, with the speaker located at a level of 30 cm. It is clear that as the frequency was raised the affected region diminished. For frequencies below 800 cps the 4-cm

layer of cotton fiber was transparent to sound. Grassy surfaces also afford only slight absorption, and therefore there were effects of interference between the direct sound and sounds reflected from the ground. This interference accounts for the irregular form of the curve for 400 cps. Also, at 400 cps the wavelength was large enough to be comparable with the width of the damping layer, and hence there was diffraction from the edges of this layer, which reduced the variation of sound pressure at the measuring point. For frequencies above 800 cps these disturbances were no longer present, as shown by the fact that a further widening of the damping layer did not affect the measurements.

Effects of an Audience upon Sound Absorption. In order to study the reductions of sound pressure produced by an audience, a number of

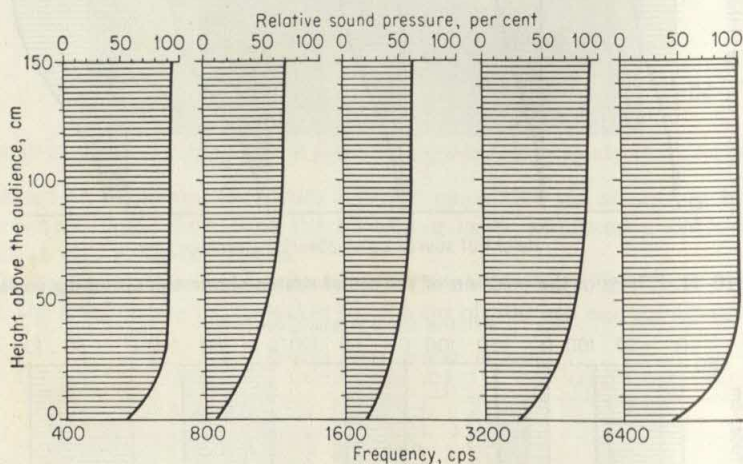


FIG. 10-36. Effect of height of the observer above the ground.

benches were placed at 70-cm distances from one another in the open air, and four persons were seated on each. A loudspeaker was located in front of the first bench at a level 40 cm above the heads of the people. An observer was in the last row, 12 meters from the loudspeaker. So as to reproduce the conditions in a theater as closely as possible, the listeners were asked to position their heads so as to keep the region of the loudspeaker in view while maintaining their assigned places. The observer used loudness comparisons to measure the changes in sound pressure. This was done by placing a phone on one ear and varying its loudness until it was equal to that coming to the open ear from the loudspeaker. A switch was used to go back and forth from one stimulus to the other. These observations, carried out by a bracketing method, were reproducible within 5 per cent, and the changes of loudness obtained were independent of the observer.

The reductions in sound pressure produced by an audience are shown in Fig. 10-36 as a function of the position above the ground that the observer took. These changes in sound pressure were closely similar to

those produced by a layer of cotton, as is to be expected, because in this region of frequency the absorption coefficient of a person is practically equal to 1.0. The only difference was that the intensity changes became less as the height above the ground was made smaller as compared with the cotton layer. This was true because for people the absorbing surfaces do not fall in one plane, but are distributed at different levels. Therefore the value obtained represents the mean of the changes produced at various heights.

If the observer took a position at the same level as the audience, there were reductions of sound intensity of the sort shown in Fig. 10-37. The attenuation was greatest in the region of 800 cps. For lower tones the absorption was found only in the immediate vicinity of the absorbing material. Also the placing of the heads of the audience so as to afford a clear view reduced the absorption at high frequencies.

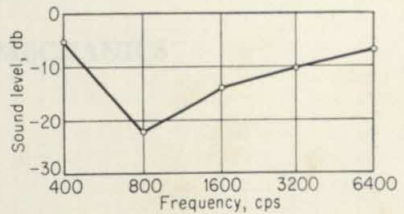


FIG. 10-37. The attenuation of the sound field for a member of the audience with his head at the general level, as a function of frequency.

The resulting frequency distortion was rather large and could easily be perceived. If a speaker was 50 cm above the audience, his voice seemed dull and impersonal in the back rows. But if the listener also was elevated 50 cm above the audience, the voice for him took on a completely different timbre, became stronger, and exhibited its individual qualities. If the audience was taken away this situation was improved still further.

It is evident that care needs to be taken to provide a listener with a free view and at the same time with an acoustic field. In this connection it seems that the reflected image from the ceiling must be utilized. If there are no such reflections, it is essential that the direct waves come to the audience at an angle that is not too small.

PART 4

THE PARTIAL COCHLEAR MECHANICS OF COCHLEAR

It is not clear whether the physical effects of the cochlear partition are best described in terms of a mechanical system. There is clearly a complex biological phenomenon of a mechanical nature, and the fact that it is a biological phenomenon is not a reason for rejecting the mechanical approach. However, for a number of reasons the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach.

The mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach.

It is not clear whether the physical effects of the cochlear partition are best described in terms of a mechanical system. There is clearly a complex biological phenomenon of a mechanical nature, and the fact that it is a biological phenomenon is not a reason for rejecting the mechanical approach. However, for a number of reasons the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach.

The mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach.

It is not clear whether the physical effects of the cochlear partition are best described in terms of a mechanical system. There is clearly a complex biological phenomenon of a mechanical nature, and the fact that it is a biological phenomenon is not a reason for rejecting the mechanical approach. However, for a number of reasons the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach.

The mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach. It is clear that the mechanical approach is not a suitable property of the cochlear partition, and it is not clear that the mechanical approach is the best approach.

CHAPTER 11

THE PATTERN OF VIBRATIONS IN THE COCHLEA

For more than a century the vibratory pattern of the cochlear partition has been the central problem of audition. There is hardly a single psychological phenomenon or clinical observation on the ear that has not served as the basis of conclusions about the pattern of action in the cochlea. Because for a century no numerical values concerning the mechanical properties of the cochlear partition were available, there were no restrictions on the imagination, and probably every possible solution of the problem was proposed. It seemed to the writer that the only way to solve the problem was to open up the cochlea and observe the action during the presentation of a tone.

This plan of experimentation was formulated on a background provided by Waetzmann's clear and objective review of earlier work. The first trial experiments were made in 1924, and the first results were published in 1928.

From the first observations of the vibrations of the cochlear partition it was clear that they represented a system about which physical science provided little knowledge and that many years would be required to understand it clearly. The first paper therefore set forth a framework for the phenomena, which would have to be filled in later with more exact descriptions and numerical values. This task is still incomplete.

In this chapter a discussion is made of the most important psychological experiments that have seemed to be in disagreement with the visual observations. It becomes clear that definite conclusions are difficult to make when there are a great many variables in the situation. Then a number of experiments are described showing that in the human ear the place of maximum stimulation along the cochlear partition changes with the frequency of the stimulating tone. Especially valuable in this relation is the study of auditory fatigue and its effects upon the pitch of a tone.

If traveling waves are present in the cochlea, then a certain time is required for the stimulation to reach all parts of the cochlear partition, depending on the velocity of those waves. Because very small time differences, of the order of 10^{-4} sec, are effective in the perception of the direction of sounds, the directional phenomena were studied as a basis for estimating the speed or "group velocity" of the waves traveling along the cochlear partition in response to a click.

Several years were required to develop the instruments needed to make

direct measurements of the elasticity of the cochlear partition along its length, the precise form of the traveling waves for low frequencies, and the displacement of the place of maximum amplitude for man and other animals. After investigation of the vibration of the cochlear partition as a whole, consideration was given to the detailed movements of its parts, with special reference to the shearing movements of the organ of Corti.

Finally, a number of models were used to portray the kinds of wave motion found in the cochlea and to bring out their differences from the waves encountered in our ordinary experience.

VIBRATORY PATTERN OF THE BASILAR MEMBRANE*

The resonance theory of Helmholtz is probably the most elegant of all theories of hearing. It assumes that the transverse fibers of the basilar membrane act as tiny resonators, each one tuned to a different frequency. The tuning varies continuously along the membrane, and stimulation by a particular tone sets in vibration only a small group of resonators in one region. The membrane is deflected only in this region, and only here are the nerve fibers excited. A tone of a different frequency involves another group of resonators at a different place and correspondingly a different nerve fiber. Thus the analysis of complex sounds is explained in a simple way.

The principal difficulty with this theory comes from the magnitude of the damping of the individual resonators. Helmholtz estimated the logarithmic decrement $\mathcal{D}$ as about 0.1. From one standpoint this damping appears to be too large to account for some of the auditory impairments arising in the cochlea. It often happens that a 10 per cent change in frequency produces a change of sensitivity of more than a hundredfold (40 db). So great a change seemingly calls for a much sharper resonance than Helmholtz allowed. On the other hand, the transverse fibers are embedded in a membranous structure and surrounded by fluid, so that from a purely anatomical standpoint even greater damping is to be expected. According to the opponents of the resonance theory the individual fibers cannot be regarded as resonators at all, but the whole membrane must be considered as a vibratory structure. This argument gains force in a consideration of certain animals, such as cats, rabbits, and birds, in which the basilar membrane is made up of two layers of fibers, one thinner than the other, rather than of only one layer, as in man (Held).

Among the nonresonance theories, Ewald's sound-pattern theory is particularly notable. According to this theory, a sinusoidal movement of the stapes sets up a series of standing waves along the basilar membrane, with wavelengths varying with the frequency. It is the task of the nervous system to resolve the separate stimuli spread out over the membrane into the impression of a single tone. A different vibratory pattern or "sound image" represents a different tone. Because the

* Article 2 as listed in the Author's Bibliography. Published in 1928.

entire task of analysis is relegated to the nervous system, whose activities are completely unknown, it is not possible to draw any further conclusions on the basis of this theory.

According to the theories of Hurst, Bonnier, ter Kuile, and Max F. Meyer, the in-and-out movements of the stapes set up on the basilar membrane a traveling wave which expires more or less rapidly depending on the conditions of damping. According to Hurst, the damping is small and the wave travels to the apex of the cochlea and back again. Therefore standing waves arise, and in this respect the theory resembles Ewald's. The further development of the theories is different, however, for Ewald is concerned with the steady state and Hurst with the transient condition. Other authors assume a greater degree of damping of the wave.

These theories seem for the most part to be in harmony with the anatomical conditions. It is more difficult to conceive of the mode of stimulation of the nerve fibers by the traveling wave. The most clear idea is that of ter Kuile, who assumes that the pitch is determined by the length of the membrane up to the point at which the wave continues to be propagated with a certain amplitude. This length is smaller for high than for low tones because of the shorter wavelength.

The important differences among the various theories consist in their different assumptions regarding the sizes of the mechanical characteristics of the basilar membrane, namely, the elasticity and friction. Only in the assumption of different values of these characteristics is it possible to derive different patterns of vibration of the membrane when the dimensions of the membrane and the manner of stimulation are the same. Therefore a choice of one theory or another can be made if the vibratory pattern of the membrane is known. Because direct observations within the cochlea are beset with extraordinary difficulties from an anatomical standpoint, the initial work was done with a model of the ear that was designed to reproduce the actual relations as closely as possible. Results from such a model should aid in making a choice among the different theories.

Model of the Ear. The width of the basilar membrane close to the stapes is about 0.1 mm and increases to about 0.5 mm at the apex of the cochlea. The fluid-filled canal above and below the basilar membrane is about 2 mm in diameter from one end of the cochlea to the other. It is difficult to carry out experiments with dimensions as small as these, and therefore it is desirable first of all to enlarge them in the model without altering any of the motional phenomena. If all of the dimensions of the model are expressed in relative numbers, based on one length l , which can be the length of the basilar membrane, then two such models with the same relative dimensions will themselves be alike. Also their motions will be similar, provided that care is taken that, despite the change in length by some factor, the equation of motion remains the same. The movement of the membrane, as well as of the surrounding fluid, is determined by a series of constants: the density ρ and viscosity η of the fluid, the frequency of movement of the stapes f , and the elasticity

of the membrane ϵ . The elasticity may be expressed as the volume displacement of the membrane per unit of length when a unit pressure is applied to one side. We shall neglect other constants, such as the density of the membrane, which differs little from that of the fluid, because they would be difficult to handle.

The equation of motion can be expressed in the form $\varphi(l, \rho, \eta, f, \epsilon) = 0$. Because the right side of this equation is dimensionless, all the constants must in the aggregate give a dimensionless product. The constant ϵ has the dimensions

$$\epsilon = \frac{\text{volume}}{\text{length} \times \text{pressure}} = m^{-1} l^3 t^2$$

and by well-known rules two dimensionless products can be formed for the whole motional equation so that

$$\Phi \left(\frac{\rho f l^2}{\eta}, \frac{\eta^2 \epsilon}{\rho l^4} \right) = 0$$

If the constants are chosen so that as we go from one model to another each product in the above equation remains constant, *i.e.*, if $\rho f l^2 / \eta$ is constant and $\eta^2 \epsilon / \rho l^4$ is constant, then the equation of motion is the same and the movements of both models are alike. From the relations just indicated it follows that for a given enlargement of the model the frequency must be decreased as the square. More important still is the limitation imposed by the elasticity of the membrane. If we assume that the rubber membrane used in the model is a membrane without internal stiffness, then it follows that, when the pressure is small, the displacement of the membrane is parabolic, and ϵ depends upon the width of the membrane d and the transverse tension τ as indicated by the formula $\epsilon = d^3 / 12\tau$, and therefore $\eta^2 d^3 / \tau \rho l^4$ is constant. Since the width d is proportional to l , it is clear that when l is made greater the tension τ must become smaller so as to maintain the same form of motion. Because the basilar membrane is a structure of great delicacy, its imitation by a rubber membrane imposes a severe limitation on the enlargement that can be given to the model. The best choice is an enlargement of four or five times. From this analysis it is obvious that the model used by Wilkinson (1), in which the basilar membrane was represented by a series of tuned brass wires coated with gelatin, is not satisfactory. An arbitrary assumption of mechanical characteristics such as these can result in any conceivable vibratory pattern.

So as to approximate the natural conditions as far as possible, the viscosity of the fluid of the inner ear was measured.* Since the human ear contains only a small drop of fluid, this was done by sucking it up into a capillary tube of 50 cm length and measuring the rate of fall when the tube was held in a vertical position. The velocity was measured over a distance of about 20 cm. If this velocity is v , the length of the falling column is l , and the radius of the capillary is r , then Poiseuille's law will

* Acknowledgment is made of the assistance of Dr. Franz Kiss and Mr. K. Frauler.

hold approximately, and the amount of fluid flowing through a cross section of the tube per unit of time is

$$V = \frac{\pi r^4 p}{8 \eta l}$$

If the pressure has the value $p = 981l\rho$, and ρ is the density of the fluid, then

$$V = 981 \frac{\pi \rho r^4}{8 \eta} = \pi r^2 v \quad \text{and} \quad v = 981 \frac{\rho r^2}{8 \eta}$$

If we consider the decrease of pressure caused by the friction of the air column that moves along the capillary with the fluid, then v must be multiplied by $[1 + \eta_0(L - l)/\eta l]$ where η_0 is the viscosity of the air and L is the total length of the capillary. The viscosity of the inner-ear fluid at 37°C when determined in this manner was the same for fresh cadavers and for others 10 days old. The mean value obtained for a long series was $\eta = 0.0197$ cgs units. Also the density of the fluid at 37°C was $\rho = 1.034$. Therefore a dilute solution of glycerin in water was used for the life-sized model, and water was used for larger models.

It is difficult to simulate the basilar membrane. It is necessary first of all to depart from the spiral coiling of the cochlea and to give the membrane a simple straight form. The coiling is not essential, because a few animals, like the anteater, have a cochlea in the form of a slightly bent tube. Likewise, Reissner's membrane can be dispensed with. This seems to be permissible because the cochlear duct, which is bounded on one side by Reissner's membrane and on the other side by the basilar membrane, is filled with a gelatinous fluid that acts in such a way as to prevent any lateral flow in response to rapidly changing movements.

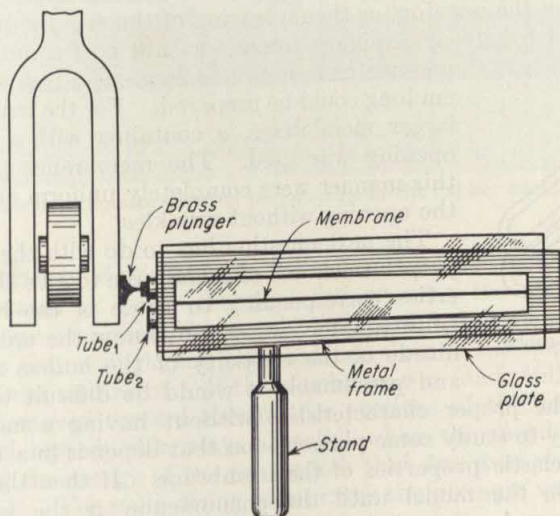


FIG. 11-1. A model of the cochlea.

Accordingly, the two membranes move in unison and can be replaced by a single one. Therefore the model was given the form seen in Fig. 11-1. In the middle of a long brass frame was fastened a thin metal band of the form shown in a top view in Fig. 11-2. The crosshatched part of the opening was covered with a rubber membrane that broadened gradually, representing the basilar membrane. The hole at one end represents the helicotrema, which in man has a diameter between 0.5 and 0.8 mm and which equalizes any static pressure variations between the two scalae.

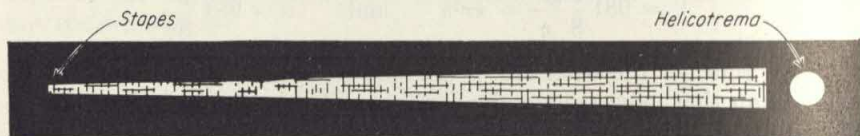


FIG. 11-2. Form of the metal band with a tapered opening which was covered with the membrane.

Two glass plates were cemented on the sides of the frame so as to fit tightly against the edges of the metal band, and the trough so formed was filled with fluid. The ends of two small tubes, representing the oval and round windows, were covered with rubber membranes, and on one of these was attached a brass plunger, representing the stapes. The plunger was attached to the prong of a tuning fork, which was driven electromagnetically by an oscillator. The whole model could be supported by means of a rod.

As in Ewald's model, the membrane was made of a rubber solution like that used by bicyclists, diluted with an equal volume of benzine. The solution was taken up with a wire loop or, for large membranes, a hook of the form shown in Fig. 11-3 and uniformly spread over the opening of the metal band. It was found best to begin the application at the narrow end of the opening, as then a tearing of the rapidly drying membrane caused by strong capillary forces was not so frequent. In this manner membranes as large as 5 mm wide and 20 cm long could be prepared. For the making of still larger membranes, a container with a slit-shaped opening was used. The membranes prepared in this manner were completely uniform and fitted in the opening without wrinkles.

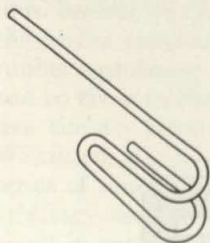


FIG. 11-3. Wire loop for applying rubber solution.

The next question has to do with the choice of a proper thickness of membrane to give elastic properties corresponding to those of the human ear. Unfortunately we do not know the order of magnitude of the elasticity of the human membrane, and presumably it would be difficult to measure.

To obtain the proper characteristics without having a measurement it is necessary to study some phenomenon that depends in a meaningful way on the elastic properties of the membrane. If then the thickness is changed in the model until the phenomenon is the same as in the ear, we can be sure that the membrane has the proper character-

istics. A phenomenon that meets the requirements was revealed by Wittmaack. He found that when guinea pigs were exposed to an intense tone there was an injury of the basilar membrane at a place corresponding to the frequency as seen in histological sections. For high tones the site of injury was close to the stapes, and for low tones it was near the helicotrema. If the intensity of the tone was not excessive, the injury was restricted to a small region of the basilar membrane.

To reproduce this phenomenon in the model, the thickness of the rubber membrane was progressively increased. It was found that, for

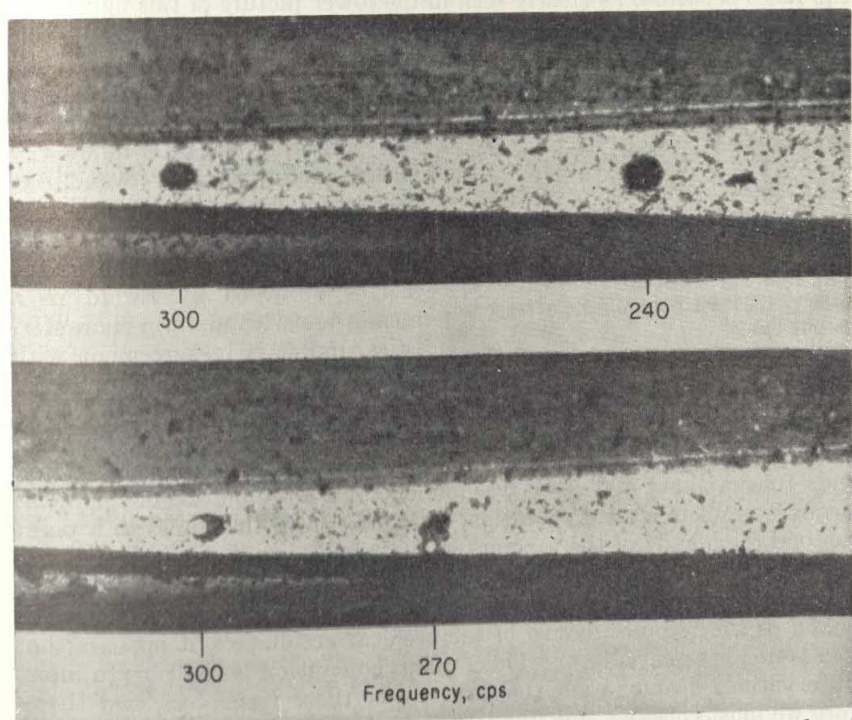


FIG. 11-4. Two experiments showing perforations in the rubber membrane produced by sounds.

a given frequency of stimulation, the thin membranes as used by Ewald were perforated in large irregular sections near the stapes. As the thickness was increased the number of perforations became smaller, until finally only a single one was produced close to the stapes where the membrane was narrowest. If the membrane was made still thicker, this perforation moved toward the broader portions of the membrane in a regular and reproducible way. Finally, when the membrane became very strong the energy of the tuning fork that was used was insufficient to damage it. For such strong membranes the pressure variations were partly equalized by way of the helicotrema.

By this method a thickness of membrane was found that for a given

tone produced a perforation at the same place as in the actual ear. The holes produced in this way were extraordinarily sharp, as may be seen in the two microphotographs of Fig. 11-4, which were obtained by the use of a model twice the natural size. The black spots represent the points of perforation of the membrane. They are black because fine carbon granules were added to the fluid to make it visible, and as a hole was formed these granules tended to stick to its edges and fill it up. This process could be observed under a microscope with stroboscopic illumination. When the amplitude of vibration was made great enough, the holes persisted, as clearly seen in the lower picture of this figure.

It is important to note that a small change of frequency resulted in two holes very close together, and this happened irrespective of whether the higher or the lower tone was presented first. This observation shows

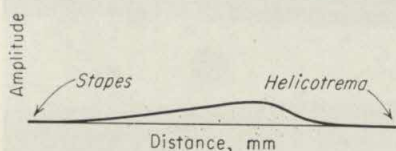


Fig. 11-5. Pattern of the vibration amplitude of the basilar membrane in response to 500 cps.

that closely adjacent portions of the membrane are little influenced in their vibrations by even large irregularities, such as the presence of a hole in the membrane. This would not be true of the sound images observed by Ewald in a membrane with uniform characteristics, but it is in agreement with

clinical experience, in which large variations of sensitivity are found for small changes of frequency.

After a membrane was chosen for the model that gave the correct pattern of response, its behavior was studied further. When stimulated by a tone of about 500 cps it was found that a large portion of the membrane was set in strong vibration, extending from the stapes to a point beyond the middle of the membrane. Only close to the helicotrema was the membrane completely motionless. The approximate values of the vibratory amplitude are shown in Fig. 11-5. If this type of curve is taken as the response curve of the cochlear resonators, it appears that the action is essentially aperiodic. This conclusion is contrary to many observations dealing with the damping of these resonators, and therefore we must consider this question further.

Damping of the Cochlear Resonators. There are two principal methods for determining the damping of a resonator. One is to record the resonance curve, and the other is to measure the transients of the vibration. A direct determination of the resonance curves for the cochlear resonators can be made only in a cochlea that has suffered disturbances of hearing due to disease, especially when the nerves have been destroyed completely over a large region of the basilar membrane. Under these conditions, a tone that only affects this portion of the membrane will not be heard at all. If then the frequency is gradually varied until the normal portion of the membrane also is set in vibration, the loudness of the tone will rise progressively until the point of maximum amplitude reaches the transverse element of the membrane where the first normal nerve fiber appears. Then as the frequency is changed

further the loudness of the tone will remain constant, for the point of maximum amplitude will be transferred to other normal nerve fibers. In this fashion we can effectively trace the half of a resonance curve of the first normal nerve fiber, either by observing the increase of loudness as a function of frequency or by finding the intensity at which the tone is barely audible. Such curves have already been obtained by several investigators, and in some instances it was possible to show by anatomical studies carried out later that the auditory impairment was due to the degeneration of a large group of nerve fibers and was not a disturbance of the mechanical characteristics of the basilar membrane. A portion of such a curve is shown in Fig. 11-6. The ordinate shows how much larger the sound pressure had to be made, relative to a normal ear, in order for the tone to be heard. The abscissa indicates the frequency. It is clear that a 10 per cent change of frequency can alter the auditory threshold by more than a thousandfold.

If this value is used in the well-known equation for the logarithmic damping of a resonant system, whereby

$$\vartheta = \pi \left(\frac{f^2}{f'^2} - 1 \right) \sqrt{\frac{1}{i_r^2/i^2 - 1}}$$

where f/f' is the mistuning and i_r/i represents the amplitude ratio between resonance and mistuning, the value of ϑ , the logarithmic decrement, is then approximately 0.0006.

That there is resonance as sharp as this is in disagreement with all other evidence, and especially with the absence of the extremely long transients of onset that this slight damping would entail. Therefore the rapid changes of acuity cannot be ascribed to a mechanical damping of the resonators. It is much more likely that the excitation of the individual nerve fibers is not proportional to the amplitude of the vibration of their corresponding regions of the basilar membrane but bears some other relation to this amplitude. This conclusion comes also from observations on the cochlear model, for otherwise it would be difficult to explain how two tones of adjacent frequency can be discriminated when the movement of the membrane is almost aperiodic.

Several methods have been used in the study of the onset time of the cochlear resonators. Hartridge used for this purpose a sudden change of phase. If a resonator is exposed to a tone whose phase is suddenly altered, say by 180° , the amplitude of the resonator falls to zero and then

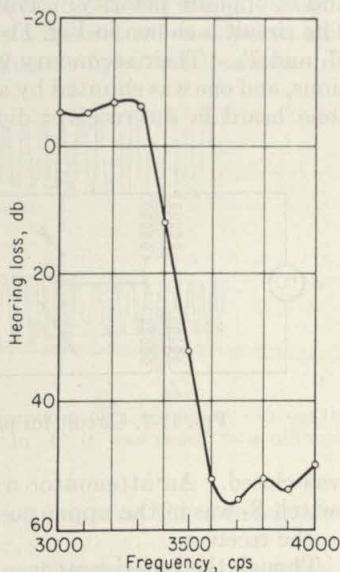


FIG. 11-6. Portion of the audiogram of a person with nerve deafness. The ordinate represents hearing loss in decibels.

builds up again. Hartridge produced the phase shift by means of a siren in which there was at one place around the disk a reduction of the spacing between the holes. He was always able to observe a clear diminution in the loudness of the tone when the phase shift occurred. These results indicated a damping of the cochlear resonators of much smaller magnitude than that of the model. Therefore his experiments were repeated.

In order to avoid transients in the room, which present a difficulty in the use of a hole siren, the sound was produced by an audio-oscillator and telephone receiver. The phase shift was produced by suddenly adding to the initial alternating voltage a second voltage of twice its magnitude and of opposite polarity. This gave a phase reversal, or a shift of 180° . The circuit is shown in Fig. 11-7. A generator G led to two transformers T_1 and T_2 . Their secondary windings were connected in opposite directions, and one was shunted by a resistance R that was adjusted so that the tone heard in the receiver did not change in loudness when switch S_1

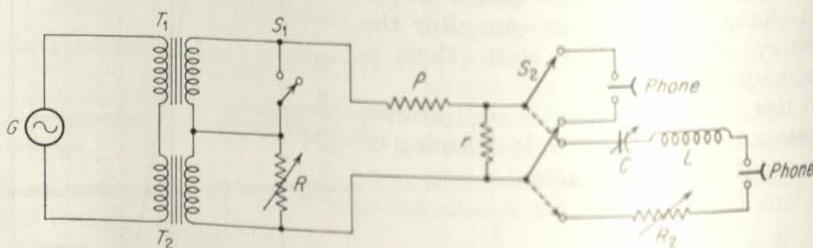


FIG. 11-7. Circuit for producing a 180° phase shift in a tone.

was closed. An attenuator was formed by ρ and r , and $\rho \gg r$. When switch S_2 was in the upper position the alternating current went directly to the receiver.

Though the experiment was repeated many times it was never possible to observe a transient change in the loudness of the tone at the moment that switch S_1 was closed. With a damping factor δ of 0.1 and a tone of a frequency of 350 cps the loudness decrease should last only 0.02 sec, and a test was made to determine whether so brief a change of intensity would be perceptible to the ear. The switch S_2 was moved to its lower position in which the receiver forms a part of a resonant circuit whose damping was calculated by the equation $\delta = 2\pi^2 f C (R_1 + r_1 + r_2 + R_2)$. The variable resistance R_2 was adjusted to give δ a value of 0.1, f was the frequency of the generator, and C was the capacity of the resonant circuit. In this situation a clear loudness variation was observed.

This transient decrease in the amplitude of a resonator that occurs when the phase is reversed can only be observed when the resonator is tuned to the stimulating frequency. If this is not so, the resonator vibrates at a smaller amplitude and increases its amplitude momentarily when the phase is reversed. The temporal course of the vibrations is indicated in Fig. 11-8. The upper curve represents a tuned resonator with a logarithmic decrement δ of 0.1, and the lower curve represents the same

resonator that has been tuned so that the amplitude during the steady state is only half that under the condition of resonance.

These relations are clearly shown in a Frahm frequency meter, which uses tuned reeds. If the polarity of the alternating current to this meter is reversed, there is a decrease in the amplitude of the reed that is in resonance with the current, and an increase in the amplitude of the reeds on either side.

In the ear there is vibration not only of the element that is tuned to the applied tone, but also of neighboring elements that are partially mistuned. The action of these other elements must be such as to produce a partial masking of the decrease in amplitude of the tuned element. Therefore we should not expect, even from a theoretical standpoint, that a phase change would have any great influence upon the loudness. In

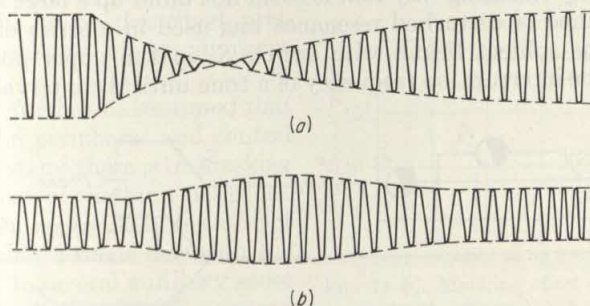


FIG. 11-8. Effect of a 180° phase shift on the response of a resonator. In (a) the resonator was tuned to the applied frequency; in (b) it was tuned to a different frequency.

any event, the observations permit us to assume that the cochlear resonators are highly damped.

The most familiar method of measuring damping is the one devised by Helmholtz. It consists of presenting short pulses of tone separated by silent intervals of equal length and finding the rate of alternation at which the onset and decay processes begin to bridge the gaps and give a continuity of sensation. From this rate the damping of the cochlear resonators can be determined.

In general a stimulus requires a certain time to be perceived, and so the question arises whether these transient processes are not produced through the sluggishness of the nerves. To determine this point, the maximum interruption rate for a tone was compared with that for a noise. With an interrupted tone the resonator repeatedly comes on and goes off with transients that tend to fill in the pauses, but with an interrupted noise various resonators work in succession in a random way so that there is no definite onset time. Therefore the interruption rate for a noise should be significantly greater than for a tone, if the cochlear resonators actually require an onset time of several cycles.

The circuit used to study this question is shown in Fig. 11-9. By means of Z_1 the alternating current from the tube generator G was

interrupted so as to produce a noise in the receiver. Z_2 is another rotating interrupter whose rate could be controlled with a counter. The switch S_1 was used to switch on the tone or the noise. To ascertain whether the interrupter Z_1 had fully converted the tone into a noise, switch S_2 could be placed in its lower position to connect a resonant circuit whose tuning could be changed to indicate whether the noise contained all frequencies of the auditory range. In order to show that for a noise the resonator does not have sufficient time to build up to a large amplitude, the damping decrement of the resonant circuit was set to $\delta = 0.1$ by means of the variable resistance. If now the resonant circuit was tuned to the stimulating frequency, the loudness of the tone in the receiver became 18 db less when the interrupter was switched in. This showed that the vibratory circuit was acted upon by the noise in such a rapidly changing way that it could not build up a large amplitude.

This method of disturbed resonance was used in a series of measurements. The subject began with switch S_2 in the upper position and increased the interruption frequency of a tone until the intervals between

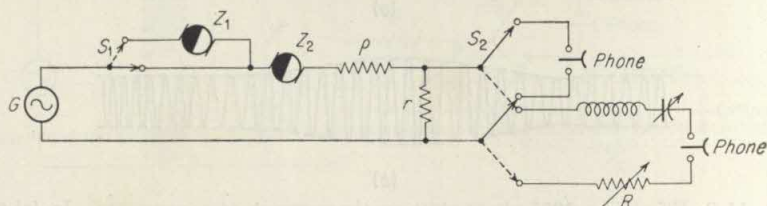


FIG. 11-9. Circuit used to present interrupted tones and noises.

pulses no longer seemed entirely empty; the subject then repeated the procedure with the noise. The ratio between the two interruption frequencies—that for the tone divided by that for the noise—for four subjects was 0.912, 1.009, 1.071, and 1.200, for a mean of 1.049.

It is clear that the tone attained the same terminal loudness as the noise. This means that there is no building up for the cochlear resonators. However, if the receiver was switched to the resonant circuit with the damping set at 0.1, the interruption frequency obtained for the tone was reduced by 1.5-fold.

From these results we may be sure that the logarithmic decrement of the cochlear resonators is considerably greater than 0.1, which agrees with the results obtained on the model.

Another way of determining the damping decrement is by studying the mutual influence of two simultaneous tones. Of special interest is the work of Wegel and Lane on masking. They showed that the threshold intensity of a tone is raised considerably when a second tone of greater loudness is present. If the masking is measured as the elevation in threshold, it is found that when the intensities used are in the normal range and do not produce appreciable nonlinearity of the ear, the masking is small for tones well separated in frequency. But if the frequency of the masked tone is made to approach that of the stronger masking tone,

the masking increases until finally beats are heard. The entrance of beats changes the phenomenon, and the masking becomes smaller. If the two frequencies coincide, we go over from masking to a loudness discrimination. If we represent masking as a function of frequency, neglecting the region where beats occur, we obtain a curve that can be regarded as a sort of resonance curve. If on the basis of this curve we are to draw any conclusions about the form of vibration of the basilar membrane, we must make the following assumptions.

First of all, we must assume that the nerve excitation at each place on the basilar membrane is proportional to the amplitude of vibration. Then a second tone of smaller amplitude can be perceived only if the increase of amplitude that it produces is a certain fraction of the amplitude already produced by the masking tone. This assumption is not very well supported as yet, in view of observations made on diseased ears and results to be described presently on contrast effects in nerve excitation.

It must further be assumed that in both the peripheral and central nervous systems there is no masking of sensations of the kind described here. This seems likely because of evidence that a single nerve fiber is connected to several auditory sense cells, so that its excitation is never restricted to one point.

Unfortunately it has not been possible so far to make a distinction between masking arising in the nerves from that arising in the form of vibration of the basilar membrane. What would be the simplest way of doing this, by putting the masking tone in one ear and the masked tone in the other, is not feasible because of the extraordinary capacity of the nervous system to keep separate the stimulations of the two ears. In such stimulation it is necessary to present the masking tone at very high amplitudes, and at these amplitudes it is conveyed to the other ear by bone conduction and masks the tone there in a direct way. Until the role of the nervous system in masking is determined, we must be cautious about our use of these results as an indication of the form of vibration of the basilar membrane.

To get an idea of the degree to which the stimulation of one ear affects the other when telephone receivers are used, let us consider Fig. 11-10. Here the ordinate shows the extent to which the threshold is raised in one ear for a given tone if the same tone is presented to the other ear at the loudness levels indicated on the abscissa. As may be seen, the intensity in one ear may be a thousand times greater than in the other ear without affecting its threshold. This curve of binaural masking agrees well with the results obtained by Wegel and Lane for various frequencies.

A method similar to the above was used by Barkhausen and Lewicki for determining the damping of the cochlear resonators. They measured

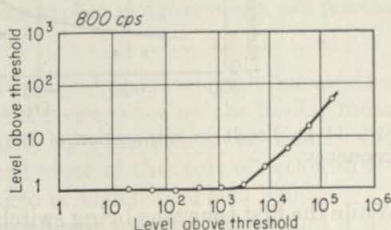


FIG. 11-10. Masking effect of a tone presented to the opposite ear.

the variations in the total loudness of two equally loud tones when their frequencies were varied. If the frequency separation of the two tones is great there is no change of loudness when one of the tones is switched on and off. When the two tones are brought closer together in frequency, however, the loudness of the two becomes greater than that of one alone and finally reaches a double value. This loudness change in relation to frequency also gives a sort of resonance curve, as shown in Fig. 11-11. Here a constant tone of 500 cps was presented along with a second tone of the same loudness but varying frequency, as shown on the abscissa.

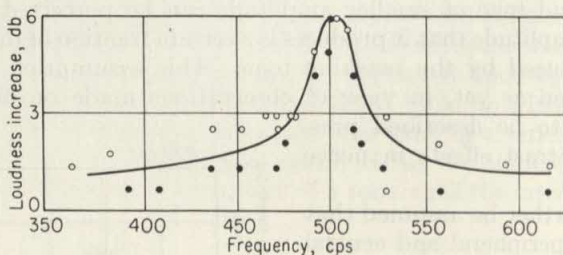


FIG. 11-11. Loudness summation of two tones as a function of their separation in frequency.

While the first tone was being switched on and off, it was found how much this tone had to be raised in intensity when sounded by itself in order for it to be perceived as equal in loudness to the two tones together. The results are shown in decibels on the ordinate. The filled and empty circles represent results from two different subjects.

A bridge circuit as shown in Fig. 11-12 was used to apply two alternating currents to the telephone receiver without any interaction between them. Here the resistance R and the induction L are matched to the effective resistance of the receiver or are replaced by a second receiver with the same characteristics.

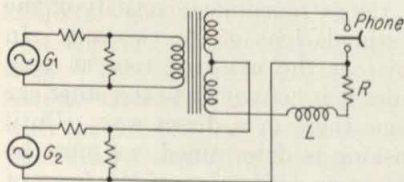


FIG. 11-12. Bridge circuit for applying two tones to one phone.

in different ears. Because of the small transmission from one ear to the other the mechanical interaction was small. Yet exactly the same form of resonance curve was obtained, as Fig. 11-13 shows.

These results prove that there is a high degree of interaction of tones in the central nervous system. Therefore it is likely that neural interaction occurs for tones at threshold in the masking situation. All the observations so far on the damping of the cochlear resonators are consistent with the assumption that the damping is nearly aperiodic, or in any case is significantly greater than $\delta = 0.1$.

Law of Contrast. Returning to the method used by Wegel and Lane for determining the form of vibration of the basilar membrane, we may raise the question whether nerve excitation in general is proportional to the mechanical action at a particular place on the basilar membrane. As we consider the nature of the nervous network in the brain, it seems likely

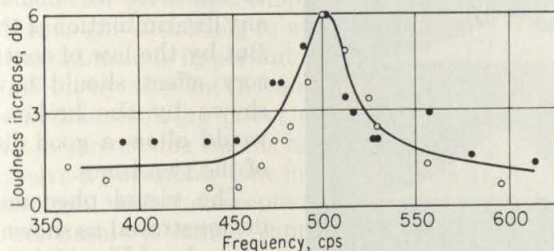


FIG. 11-13. Loudness summation for two tones applied to different ears, as a function of frequency.

that the nerve fibers forming this network can interact with one another so that the operation of a stimulus at a given place on the basilar membrane can be affected by the intensity of stimulation on either side. Mach (2) was the first to bring forward proof of this sort of action in the field of vision (see also Köhl).

Thus it may be shown that a distribution of stimulus intensity such as that represented in *a* of Fig. 11-14 produces a sensory effect like that shown in *b*. A dark spot is seen at each place where the light intensity was changing in such a way as to give a curve that is concave upward as in *A* of the figure. Here the brightness seems to be suddenly diminished.

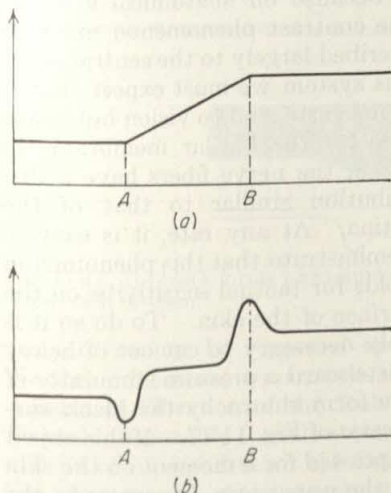


FIG. 11-14. (*a*) is a form of distribution of light intensity and (*b*) its visual effect.

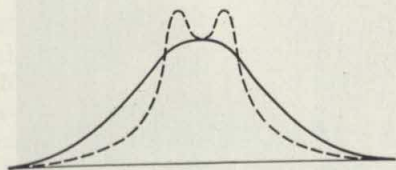
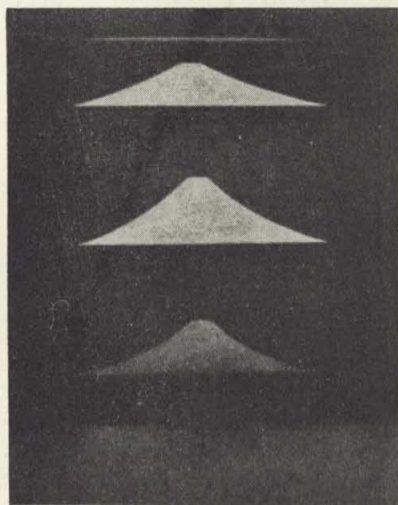


FIG. 11-15. A form of distribution of amplitude on the basilar membrane (solid line) and its expected sensory effect (broken line).

On the other hand, at places where the curve of light intensity is concave downward, as at *B*, there is an apparent increase of brightness. These departures from the actual brightness distribution are not small but are of the order of magnitude of the brightness itself. Therefore the experienced distribution of brightness departs markedly from that

presented. Let us consider a distribution of brightness corresponding to the form of stimulation of the basilar membrane produced by two simultaneous tones of closely similar frequency. Then the two resonance curves will fuse to give a peak region with uniform amplitude as shown



by the solid curve of Fig. 11-15. In this case we should not expect any discrimination of the two tones. But by the law of contrast the sensory effect should have the form shown by the broken line, which would allow a good discrimination of the two tones.

The visual phenomenon can be demonstrated as shown in the photographs of Fig. 11-16. On a black cylinder were mounted white areas of the form of the resonance curves described above, and when the cylinder was rotated a band of light was seen with two distinct white stripes in the center.

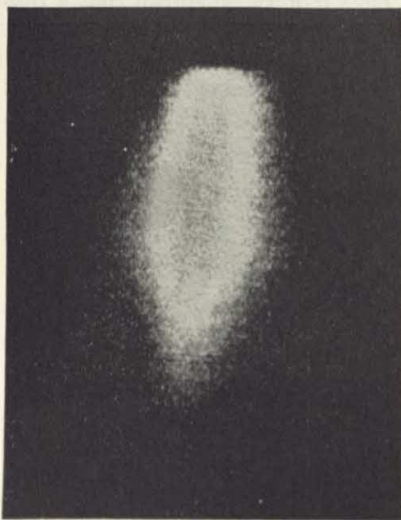


FIG. 11-16. The white areas (above) when rotated gave the visual effect as indicated (below).

Because from anatomical grounds the contrast phenomenon must be ascribed largely to the central nervous system we must expect that it is not restricted to vision but holds also for the basilar membrane, in which the nerve fibers have a distribution similar to that of the retina. At any rate, it is easy to demonstrate that this phenomenon holds for tactual sensitivity on the surface of the skin. To do so it is only necessary to cut out of heavy pasteboard a pressure stimulator of the form shown by the black surfaces *a* of Fig. 11-17. If this object is pressed for a moment on the skin of the upper arm, for example, the sensation does not correspond to the form of the stimulus, but is like that represented in *b*, which clearly is a contrast effect. This experiment does not always give a proper

result because the object stimulates not only the skin nerves but also the nerves in the underlying muscle layers.

Therefore it appears that Mach's law of contrast should play a highly significant role in auditory theory. It achieves a certain patterning of

sensation, as in the example just described. A distribution of stimulation with the form of a single resonance curve will produce a high peaking of the maximum, because at this point the stimulus intensity undergoes its greatest variation, whereas on either side the stimulus effect falls off and the curve there is convex downward.

The law of contrast gives firm support to the hypothesis advanced by Fischer and Budde (2), according to which only the maximum amplitude of the basilar membrane is important in stimulation. At the same time this contrast effect, by altering the amplitude pattern, produces a significant increase in the resolving power of the ear. Without it we should have difficulty in accounting for the interaction of two tones and for our ability to perceive a particular tone in a chord.

We now have seen that the acceptance of nearly aperiodic damping for the cochlear resonators is largely supported by the evidence, though the

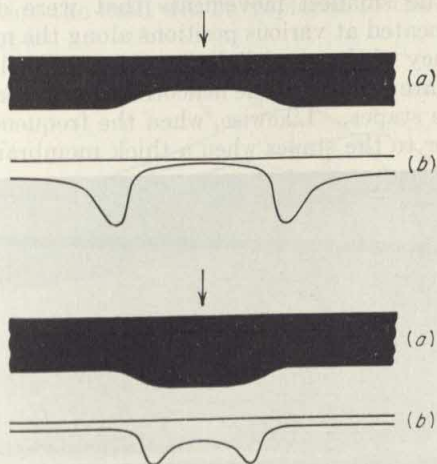


FIG. 11-17. The black forms when applied to the skin gave the tactual effects indicated below each of them.

problem cannot be regarded as settled without further investigation. We therefore return to our consideration of the cochlear model.

Form of Vibration of the Rubber Membrane in the Cochlear Model.

To make it possible to follow the movements of the fluid of the model as well as of its membrane, the fluid was filled with fine carbon particles. For photography of the movements, finely ground aluminum foil or gold leaf was used. When the tuning fork was set in vibration, this dust which was resting on the membrane was rapidly transported from the stapes to the helicotrema. This fact showed that a traveling wave was present, going in the direction of the helicotrema. When after a moment the steady state was reached, the fluid in the neighborhood of the helicotrema came to rest, and even a great increase in the stimulation gave no observable movement of the particles. There was an equalization of the total pressure variations above the basilar membrane, so that over the helicotrema in particular there were no movements of the fluid.

On the other hand, two sharp eddies were formed above and below the membrane in a particular region as in Fig. 11-18. The photograph of Fig. 11-19 shows the two eddies, and it may also be noted that the aluminum powder was mainly deposited in the region of the helicotrema. In photographs the eddies do not show up as sharply as they really were

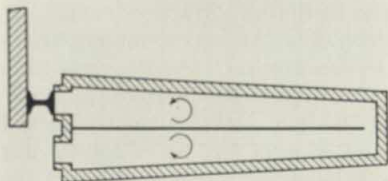


FIG. 11-18. Form of eddies in the cochlear model.

because the strong light required at the high magnification caused a warming up on one side and produced a slow movement of the fluid. The diameter of the eddy was always equal to the height of the fluid above the membrane, and its velocity of rotation was proportional to the amplitude of motion of the stapes down to the smallest movements that were detectable.

The eddy was located at various positions along the membrane according to the frequency of the stapedial vibrations. For low frequencies it was in the immediate vicinity of the helicotrema, and for high frequencies it was close to the stapes. Likewise, when the frequency was kept constant, it was closer to the stapes when a thick membrane was used than

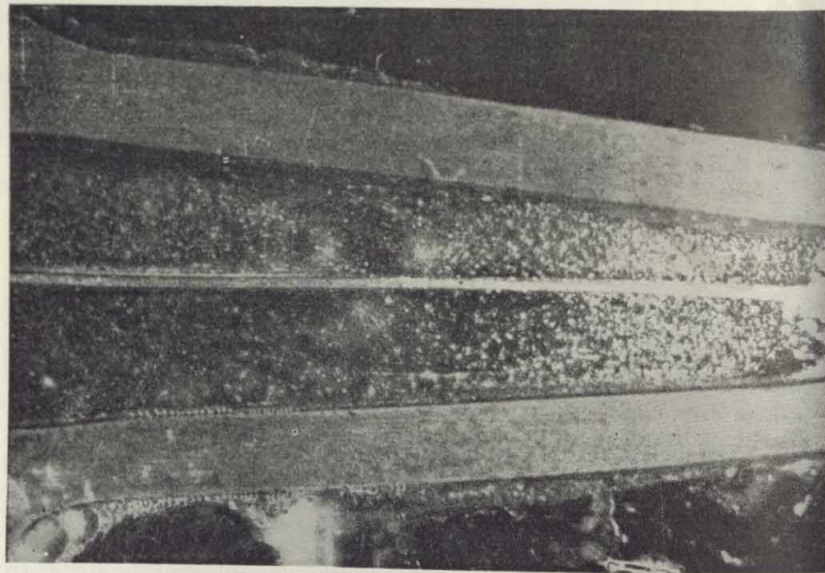


FIG. 11-19. Photograph of the eddies.

for a thinner one. Because the rubber membrane absorbed water in high degree, its elasticity diminished greatly with time, and accordingly the eddy moved toward the stapes.

The production of this eddy is simply explained. In an approximate way we can consider the rubber membrane as divided into several transverse bands, much as conceived of in the resonance theory. Let us

suppose that these bands are equal in width (*i.e.*, as measured along the longitudinal dimension of the membrane); but they vary in length at different places along the membrane. Then they can be regarded as separate resonators whose natural frequencies decrease continuously toward the helicotrema. If this system of resonators is exposed to sinusoidal stimulation, the amplitudes of vibration at successive instants will form a group of curves like that of Fig. 11-20. If the stapes is in the extreme right position, the membrane is bulged strongly downward. If now the stapes moves to the left, the membrane will gradually bulge upward, taking positions at successive instants as indicated by curves 1 to 6.

From the intermediate curves it may be seen that in the course of this movement the fluid above the membrane and on the left side will be sucked in the direction of the solid arrows. When the membrane reverses its direction the fluid will be displaced to the right as indicated by the broken arrows.

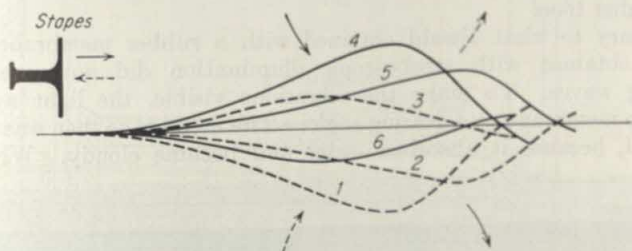


FIG. 11-20. Curves showing successive patterns of amplitude on the basilar membrane of the model during a full sinusoidal vibration.

In this manner the vibration of the membrane near the place of resonance, where the displacement is the greatest, produces a transporting of fluid near the surface in a direction from the higher tuned resonators to the lower tuned ones. This transported fluid of course must return, and in this way the eddy arises. The same thing takes place on the lower side of the membrane, though the form of motion is a mirror image of that on the upper side. This situation accounts for the variation in the location of the eddy as a function of frequency, as well as for the other phenomena mentioned. Because the vibration has its maximum amplitude at the place where the eddy appears, a perforation of the membrane always occurs there.

The movement of the membrane can be followed precisely through the observation of the carbon particles under the microscope with stroboscopic illumination, if the interruption of the light is adjusted so that the membrane seems to execute about one vibration per second. It then is clearly seen that the membrane does not vibrate with standing waves, but that the waves are propagated continuously toward the helicotrema, where they rapidly lose their amplitude.

A picture of the form assumed by the membrane at a particular instant is given in Fig. 11-21. The portion of the membrane from the stapes to

the place of resonance vibrates almost completely in the same phase. At the place of resonance there appears a phase reversal, and from here on waves arise that with a uniform rubber membrane become progressively smaller in wavelength. At the place where these waves begin, the eddy movement of the fluid ceases, and in this region the fluid only moves to and fro, as the arrows indicate. In Fig. 11-22 is shown a

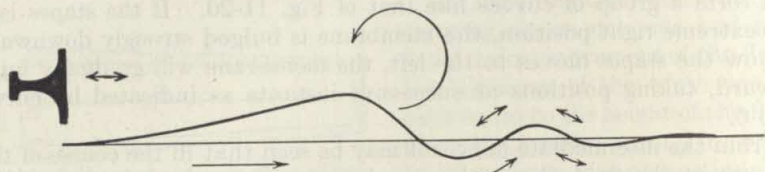


FIG. 11-21. Vibration pattern of the basilar membrane and the eddy effects in the surrounding fluid.

photograph of the form of movement of the membrane for a lower and for a higher tone.

Contrary to what Ewald obtained with a rubber membrane, these results obtained with stroboscopic illumination did not reveal any standing waves. To make the vibrations visible, the light was cast upon the membrane at a grazing angle. The membrane then was readily observed, because it absorbed water and became cloudy. When the

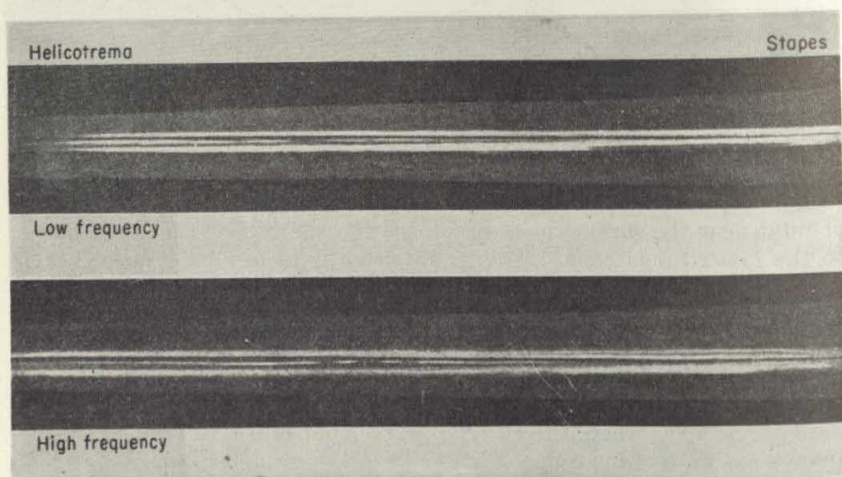


FIG. 11-22. Photographs of the model in response to two frequencies.

waves were produced, their valleys fell in the shadow of the metal frame and so seemed dark. Therefore the deflections of the membrane were readily perceived.

To discover to what extent the cochlear duct influences the form of vibration of the membrane, a second model was constructed in which Reissner's membrane and the cochlear duct were represented as in Fig. 11-23. Reissner's membrane was formed as an extremely thin membrane

stretched over a small frame, so that its elasticity was small in comparison with the basilar membrane, and therefore it had little influence on the action. By means of a funnel the space between the two membranes was filled with a viscous fluid, either glycerin or honey, so as to reproduce the mass present in the cochlear duct. Also a small hole was drilled on one side to represent the helicotrema.

It was found that the form of vibration of the basilar membrane was much the same as before, except that the number of waves that could be seen was usually reduced to two because of the increased damping. The eddy over the basilar membrane was visible as before. Also there was a broader one below Reissner's membrane, which signified that on account of the great viscosity of the fluid for rapid vibrations the two membranes vibrated together.

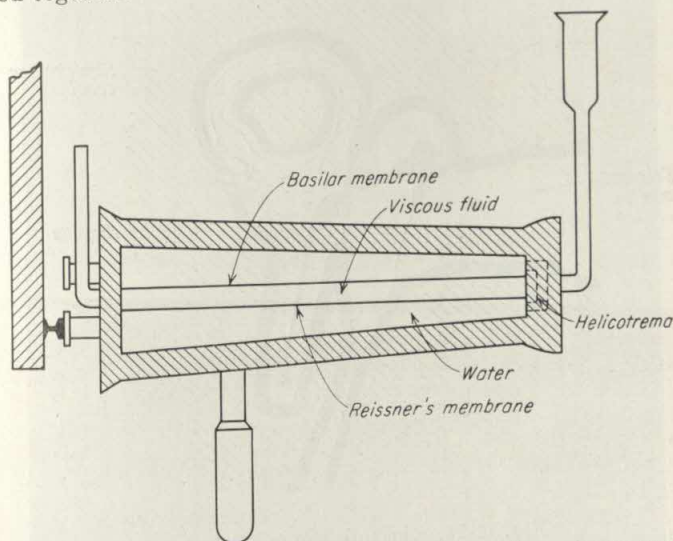


FIG. 11-23. A cochlear model in which Reissner's membrane is represented.

The experiments showed further that a perforation of the membrane no longer occurred at a point, but always a large area was destroyed. This also agrees with observations made on the ear itself.

After these relations had become sufficiently understood on the model, the investigation was continued to determine whether the human basilar membrane undergoes movements of the same kind.

Form of Vibration of the Basilar Membrane. In the study of the question whether eddies or a strong flow of fluid along the basilar membrane result from the action of intense tones upon the ear, let us consider Fig. 11-24. This is a schematic cross section of the inner ear showing the cochlea and the vertical semicircular canal with its ampulla. As is well known, the semicircular canals and ampullae in man serve for the perception of equilibrium. If the onset of a strong tone actually sets up a streaming of the fluid along the basilar membrane in the manner

indicated in the figure, this movement must involve not only the fluid of the cochlea but that of the canals as well. This will be true because the canals are connected to the cochlea at two different places, so that the fluid movement will set up a pressure difference between these two openings.

Such a streaming of fluid in a canal will produce a disturbance of equilibrium, which will cause the head to be inclined to the right or the left. To ascertain the direction of this inclination a familiar physiological method was used, consisting of the injection of cold water upon the eardrum. This injection causes the fluid in the part of the semicircular canal lying near the eardrum to be cooled off, whereupon it sinks, causing a tipping of the head in the direction of the eardrum. Then if, as the

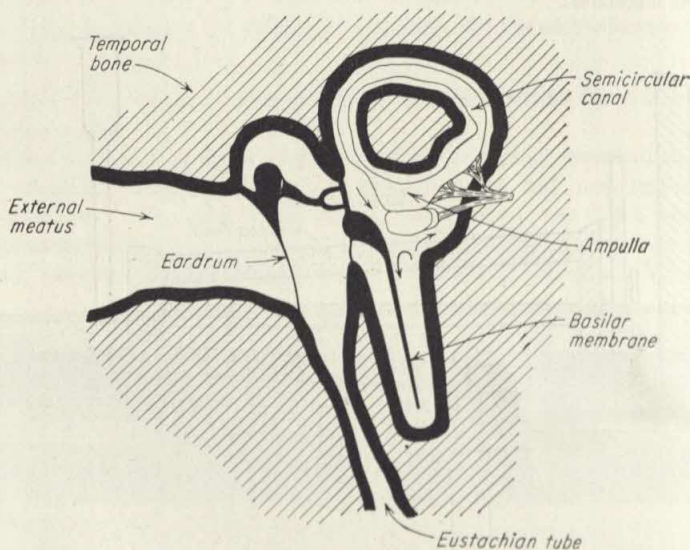


FIG. 11-24. Schematic section of the ear.

arrow of Fig. 11-24 indicates, the introduction of a tone produces the same streaming in the canal, a tipping of the head must follow. If the tone is intense (near the threshold of feeling), then overtones will arise through the nonlinearity of the eardrum and the cochlea. They will produce a spreading of the eddy toward the stapes, so that during the sounding of the tone the streaming will remain in the region of the canal. Then if the tone is switched off, the fluid motion in the canal will cease, and the head will move to the opposite side. Both of these reflex movements could be demonstrated, though an unpracticed subject usually perceived the second one more readily. This was true because only after a little practice could the reflex movement arising from the fluid streaming in the canal be distinguished from the usual response of withdrawal from a sudden tone. However, if a person is accustomed to listening to strong tones, these two effects are observed with confidence.

This physiological investigation leads to the conclusion that during

stimulation a traveling wave is formed on the basilar membrane, and not standing waves. The following procedure was used to confirm this conclusion by direct observation.

A temporal bone from a fresh cadaver was freed of all unnecessary tissues, and the apex of the cochlea was ground down with a fine grinding device until a small opening appeared, but without any damage to the basilar membrane or Reissner's membrane. This grinding is difficult and is successful only occasionally even when done with the greatest

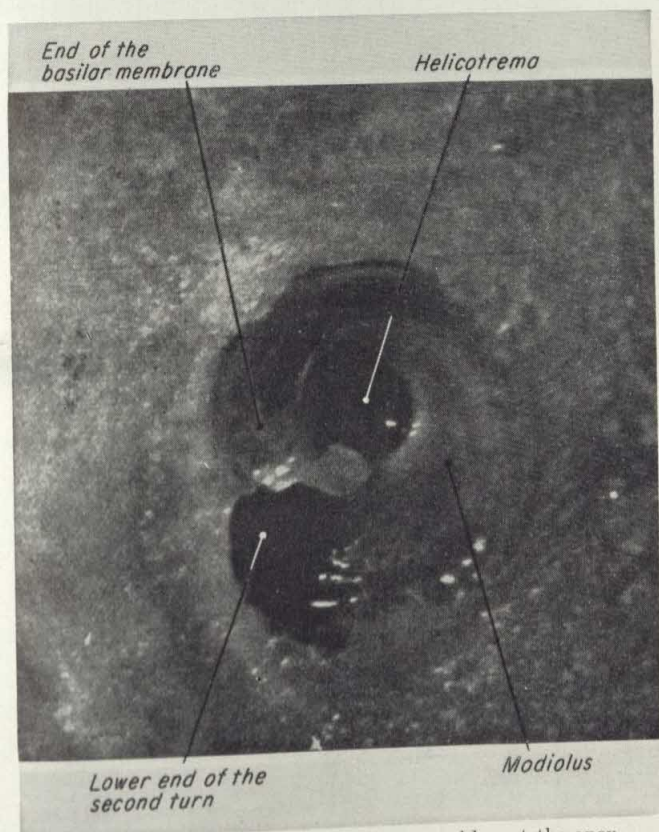


FIG. 11-25. Method of opening the cochlea at the apex.

care. Therefore it is helpful, especially at first, to soften the bone by decalcification at the place where the opening is to be made. This is particularly necessary because there are large differences among specimens in the spatial relations within the cochlea, and even considerable experience with this situation is insufficient. The method of grinding is illustrated in Fig. 11-25, which shows clearly that no membrane has been damaged or displaced from its proper position. The cochlea contains about $2\frac{3}{4}$ turns, and as one turn has been brought into view, about one-third of the basilar membrane has been exposed.

The two membranes are almost completely transparent, and to make their movements visible it is necessary to apply some carbon or aluminum powder to them. A little of the powder was added to dilute saline solution and injected into the cochlea. The powder then settled down on the membranes. After the cochlea was completely filled, a small glass plate was glued over the opening as shown in Fig. 11-26.

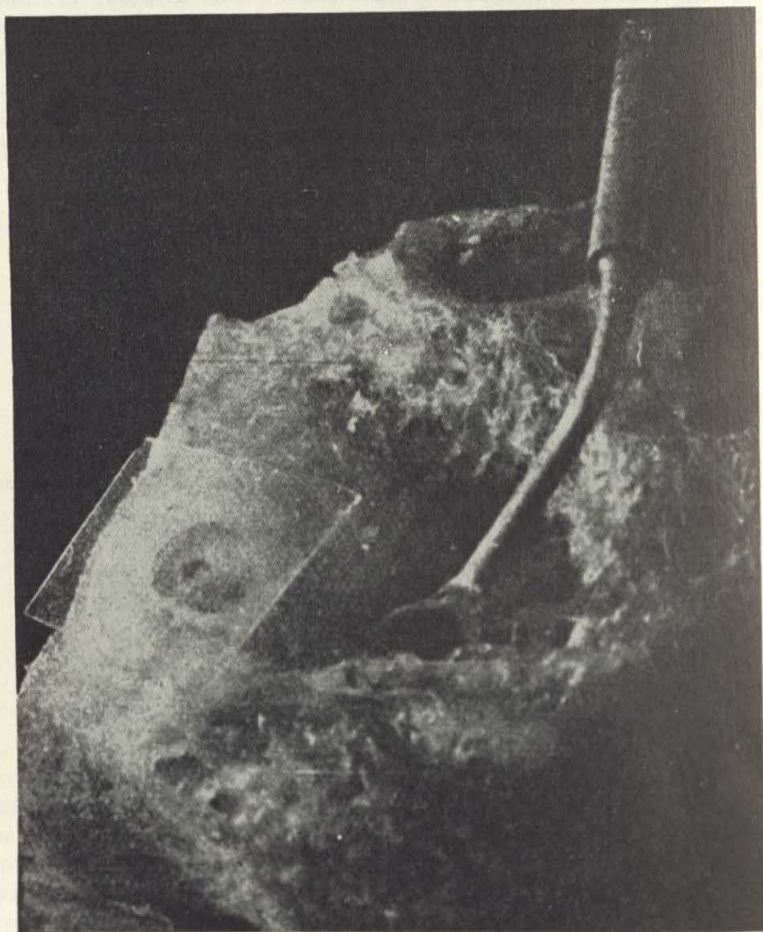


FIG. 11-26. Method of covering the opening with a glass plate.

Often during the grinding some of the fluid escaped from the deeper regions of the cochlea, and then a bubble remained after the cochlea was filled. These bubbles usually came out readily if before the closure there was a momentary stimulation of the stapes, because the fluid movement just described progresses along the membrane. If this procedure was unsuccessful, a little alcohol was added to the fluid and the cochlea carefully warmed up, as by bringing it into the beam of an arc lamp.

Next the ossicles were removed up to the stapes, and to the stapes a fine wire was carefully cemented, as shown in Fig. 11-26. This wire led to one prong of an electromagnetically actuated tuning fork. When the tuning fork was set in vibration the movements of the basilar membrane could be observed with a microscope. For more exact investigations stroboscopic illumination was always used.

Often the experiment was brought to a close, especially when strong amplitudes were used, by a ripping of the stapes out of the oval window. In order to continue the observations in spite of this, the tube system shown in Fig. 11-27 was used, and its lower end was sealed to the bony edges of the oval window. The enlarged end of this tube was connected to a rubber diaphragm which was set in motion by a small piston, now acting as a stapes.

To be certain of avoiding any air bubbles in the cochlea, the glass window at the apex was removed, and a funnel was used to force fluid slowly through the entire tube system until all bubbles were removed. Then the apical opening was sealed once more, and the stopcock on the funnel was closed. This arrangement had the advantage of permitting much greater amplitudes of vibration of the basilar membrane, so that observations could be made with a lower power of the microscope, and thus with a broader field of view in which the whole membrane was seen at one time.

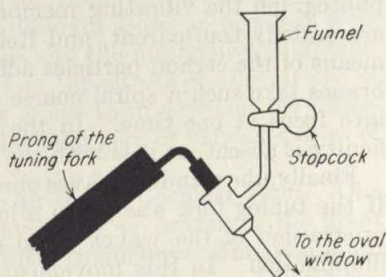


FIG. 11-27. The artificial stapes.

Because this artificial tube system lengthens one scala of the cochlea, the question arises as to whether it affects the form of movement of the basilar membrane. To test this point a model was constructed with the membranes situated at different places in the chamber. It was found on stimulating with the tuning fork that despite the difference in position the two membranes showed eddies in practically the same places. This observation shows that the length of the fluid column over which the pressure variations are conducted to the membrane has only an insignificant effect upon the location of the place of resonance of the membrane. The same thing was observed when a large mass of lead was attached to the round-window membrane, thereby effectively lengthening the fluid column in this scala. In this experiment there was no noticeable displacement of the mid-point of the eddy. Hence we may be sure that the artificial tube system had no qualitative effect upon the form of vibration of the basilar membrane.

This limited influence of the length of the fluid column on the place of resonance of the basilar membrane seems not to confirm an assumption made by Lux, according to which the natural frequency of any one portion of the membrane is determined by the elasticity of the membrane and by the mass of vibrating fluid extending from the stapes to the point of resonance on one side of the membrane and from the resonance point to

the round window on the other side. The reason for this is perhaps to be found in the fact that not only does the fluid move in this accepted sense, but that on this movement is superimposed a vibration of the fluid that takes place between a peak and valley of the wave as shown on the right of Fig. 11-21. The mass of fluid concerned in this vibration is dependent merely on the local elasticity of the membrane. Hence the place of resonance of the membrane also is independent of the vibratory conditions present at other places.

Ewald (3) has already carried out direct observations of the vibrations of the basilar membrane of the guinea pig. However, his report contains only a few lines, and it is not possible to discover how the experiment was performed.

Apparently Ewald removed a portion of the basilar membrane from the cochlea and placed it in his "camera acustica" to set it into vibration. Otherwise it is difficult to understand his remark that he was able to photograph the vibrating membrane. In the cochlea both membranes are entirely transparent, and Reissner's membrane can only be seen by means of the carbon particles adhering to it. Moreover, the two membranes take such a spiral course that only a small part can be brought into focus at one time. In the "acoustic camera," however, this difficulty is absent, as it is with the rubber membrane.

Finally, the standing waves observed by Ewald could not be confirmed. If the tuning fork was given a low frequency, say, of about 200 cps, a progression of the waves could clearly be observed with stroboscopic illumination. In this movement Reissner's membrane and the basilar membrane were synchronized. The damping was so great that only one wave at most could be clearly made out. If a higher frequency was used, the part of the membrane that was visible in this experiment remained completely at rest.

Hence there is qualitative agreement between the movement of the membrane in the model of the cochlea and in the actual human ear.

The manner in which vibration of the membrane produces stimulation of the nerve fibers will not be considered at length here. One possibility is that the pressure effect of the eddy acts upon the basilar membrane, in which case the stimulation zone for a pure tone will extend over a rather narrow region, and apparently this region will be restricted further by a contrast effect.

In this relation Reissner's membrane will act so as to reduce the pressure on one side of the basilar membrane, and therefore the steady pressure on the other side, working against the resistance of the cochlear duct, will produce a bulging of the membrane.

Accordingly, the ear is to be regarded as an aperiodic frequency analyzer of a sort yet unknown in technology. How the analysis differs basically from that achieved by usual methods can best be seen by considering multiple-frequency telegraphy. In this method the frequencies are separated by means of individual receivers tuned to particular frequencies, and because transients are always present in the response of such receivers the speed with which messages can be sent is seriously decreased.

In the ear, on the other hand, an aperiodic form of communication is achieved.

Moreover, the appearance of eddies represents an effective rectification of the vibratory movement of the fluid. Therefore it may easily explain the appearance of combination tones.

VIBRATIONS OF THE COCHLEAR PARTITION IN PREPARATIONS AND MODELS*

Now to be considered are the patterns of vibration of the cochlear partition as measured in fresh preparations of the human ear during stimulation by pure tones. To observe these patterns it is necessary to drill holes through the bony wall of the cochlea and then to cover these holes with glass windows. The covering procedure is particularly difficult, and preliminary observations were made on models to discover whether it is really necessary. With the models the changes in the vibratory pattern were measured when different types of openings were made. At the same time, the dimensions and the mechanical characteristics of the model were varied to ascertain the effects on the pattern of vibration. These observations make it easier to understand the differences that exist in the construction of the inner ears of various species of animals.

Transmission of Vibrations from the Air to the Cochlear Fluid. One of the most peculiar features of the physiology of hearing is the great variation in the auditory threshold with frequency. The minimum audible pressure for a tone of 1000 cps is about ten thousand times less than for a tone of 25 cps. The question is raised whether the variation with frequency arises in the mechanical transmission of the sound pressure from the air to the cochlear fluid, or whether it is correlated with some variation in neural excitation in the inner ear.

In the attempt to answer this question, measurements were made of the displacements of the round-window membrane for various frequencies and a given sound pressure at the eardrum. The round-window membrane is round, as its name implies, and it lies deep in a niche that makes it difficult to approach. Its area is about 2 sq mm. Also this membrane is covered by a thin secondary membrane, so that the usual methods of measuring the amplitudes of vibrating bodies are not applicable. Therefore the following method was employed. One arm of a small T tube was cemented to the edge of the niche, and to the stem of this tube a small earphone from a hearing aid was fastened. On the other arm was attached a small rubber tube, the other end of which was led to the ear of an observer. Sound pressure on the eardrum of the preparation produced movements of the round-window membrane in the niche. These movements produced a sound in the ear of the observer. A sound produced by the earphone was made to compensate for the sound produced by the movements of the round-window membrane, so that the observer was no longer able to hear the tone. When this occurred, the

* Article 42 as listed in the Author's Bibliography. Published in 1942.

diaphragm of the earphone had the same volume displacement as that of the round window, and the two membranes were vibrating in opposite phase. From a calibration of the diaphragm of the earphone the volume displacement of the round window was determined.

An easy way to make a hole in the middle ear just opposite the round window is to start from the facial canal, as shown in Fig. 11-28. This canal lies at the base of the styloid process and was found by probing with a needle. A needle in this canal located a plane passing through the needle and the middle of the mastoid process. The direction of the drill used to open the middle ear was then fixed in this plane parallel to the direction of the needle and 6 mm away from the facial canal toward the

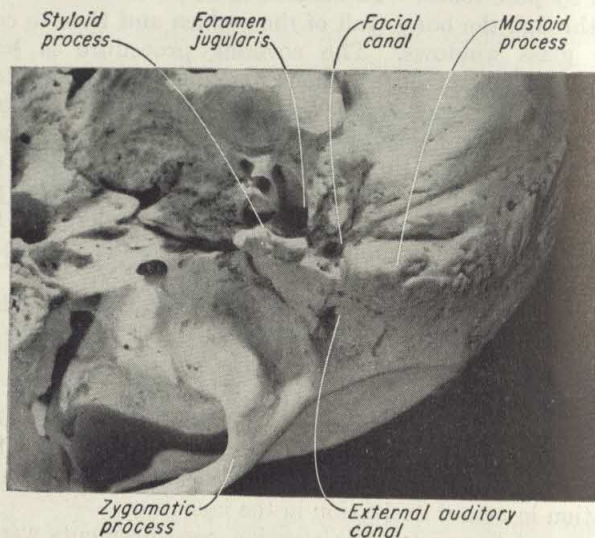


FIG. 11-28. The base of the skull, seen from below.

center of the head. By opening the wall of the jugular foramen a hole was obtained opposite the round window. In order to indicate clearly the directions of the two holes, a small piece of wire was bent into a U shape with the two prongs 6 mm apart. The prong shown on the right in Fig. 11-29 was inserted into the facial canal. Both prongs lie in a plane passing through the middle of the mastoid bone, and the left prong then comes just opposite the niche of the round window.

After the round window had been located exactly, the opening into the middle ear was enlarged. With the aid of a microscope the membranes on the edge of the niche were removed and a wall of dental cement was formed around this rim. It was necessary that the cement mixture be stiff enough to hold its shape. After the cement had hardened, a short tube was fastened to this rim, and then the outside of the tube was cemented to the hole in the wall of the middle ear so that the middle ear was again airtight. A second tube equipped with a small condenser microphone was cemented into the external meatus, as shown in Fig.

11-30. This tube served to lead the sound to the eardrum. In order to measure the displacement of the round window, the tube coming from the round window, as well as the whole temporal bone, was cemented to a heavy lead base. In this lead base there was mounted the earphone and the tube that led to the ear of the observer. As can be seen from Fig. 11-30, a movement of the eardrum of the preparation produced a movement of the fluid in the cochlea. This moved the round-window membrane, which moved the air in the tubing and in turn produced a sound in the ear of the observer. Therefore the sound heard by the

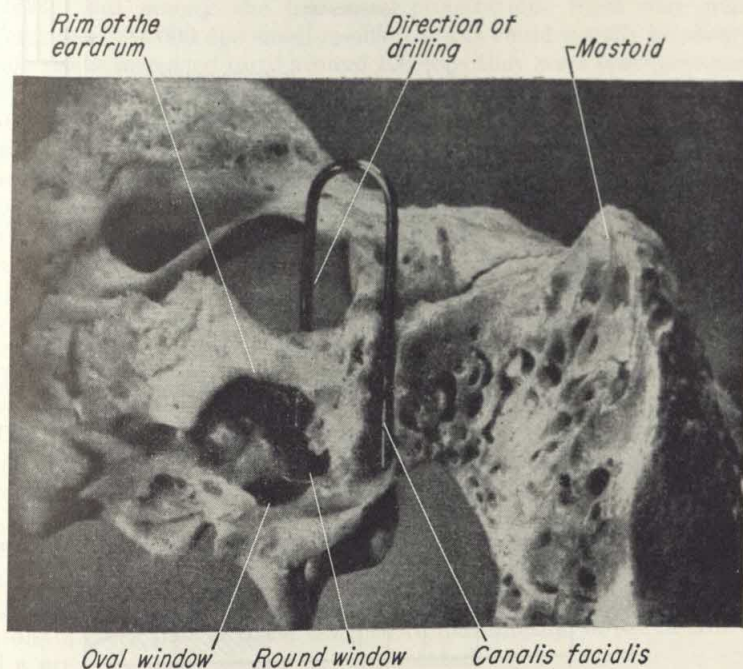


FIG. 11-29. Bent wire used to locate the round-window niche.

observer was a measure of the movements of the round-window membrane. In order to prove that the sound heard was caused only by movements of the round-window membrane relative to the bony part of the inner ear and not by movements of the whole temporal bone, the round window was filled with cement, with the result that sound was no longer heard.

It is important that the distance between the eardrum of the preparation and the condenser microphone (in Fig. 11-30) be as small as possible in order to reduce the possibility of standing waves. The same holds for the distance between the round window and the earphone. In an effort to reduce even more the possibility of standing waves, the tubing was filled with hydrogen.

By the method described, the volume displacement of the round-

window membrane was compensated for, and thereby the ratio of the volume displacement of the round window to the sound pressure on the eardrum ($\Delta V/p$) was obtained. The results are given in the lower curve

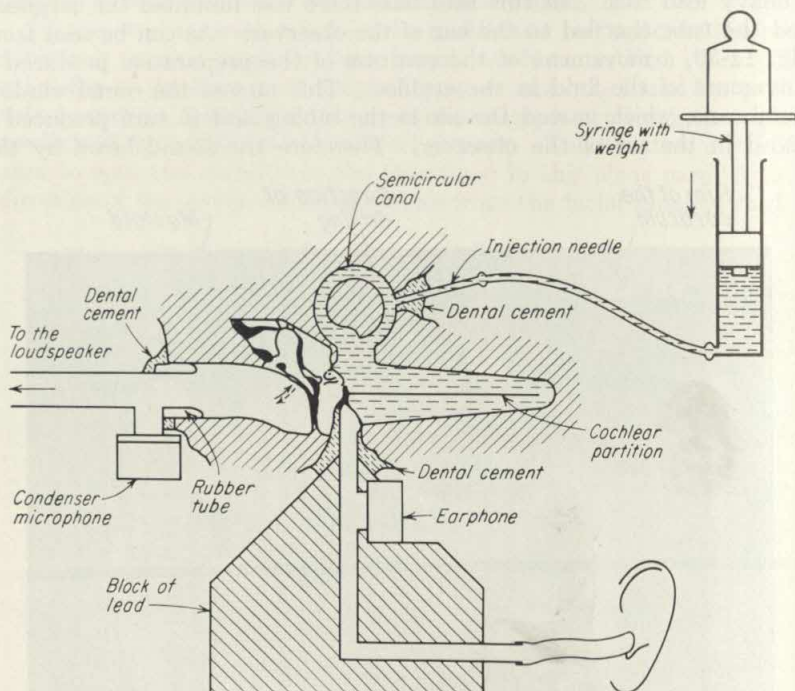


FIG. 11-30. Method of fitting the stimulating and recording equipment to the temporal bone.

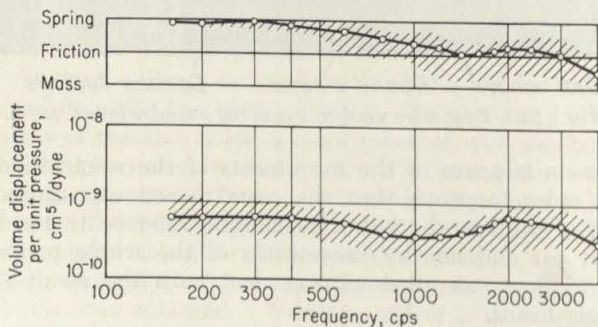


FIG. 11-31. The responses of the round-window membrane to sound. The upper curve shows the phase angle and the lower curve the volume displacement per unit of pressure.

of Fig. 11-31. The upper curve shows the phase angle between the sound pressure on the eardrum and the displacement of the round window. For low frequencies the movement of the round-window membrane represents an elasticity. For higher frequencies the influence of the viscosity is

predominant. And finally, for frequencies above 3000 cps the phase angle shows an inertia effect. The lower curve indicates that the absolute value of the vibrations of the round window for a constant sound pressure on the eardrum is practically independent of the frequency in the range from 150 to 4000 cps. This suggests that the large differences in the thresholds of hearing for various frequencies are due to mechanical effects inside the cochlea or to some characteristics of nervous excitation.

Measurements made over a period of two weeks showed no important changes for a temporal bone kept in Lysol solution at a temperature of 5°C. But among the individual preparations there were marked differences. At 600 cps small resonant peaks could usually be observed. These peaks increased until around 1200 cps they were often pronounced and showed distinct individual characteristics. Therefore it is possible that the little peaks that appear in precise threshold measurements, as shown especially by Waetzmänn (9; Waetzmänn and Keibs, 1), are caused mechanically by the middle-ear ossicles, which have characteristics as personal as facial features. The two ears of the same skull have closely similar resonant peaks. Individual differences in the eighty different temporal-bone preparations were obvious. The surface area of the round-window membrane, for instance, varied over a range of 1:3, and its thickness varied even more. The range of variation of the volume displacement of the round-window membrane is shown by the crosshatching in Fig. 11-31. Some of the sharpest resonant peaks around 1200 cps have been omitted.

The method commonly used for testing the mobility of the ossicles by pulling on them with forceps does not allow us to draw any conclusions about the behavior of the ossicles while vibrating. Measurements of the amplitude of vibration of the round-window membrane appear, therefore, to be particularly useful in a systematic investigation of the mobility of the middle-ear mechanism in different types of disease. In this way it is possible, at least during autopsy, to delimit sharply the portion of the disturbance that is to be assigned to malfunction of the middle ear, and a previous diagnosis can be corroborated.

It has been said that a high static pressure in the cochlea produces an outward displacement of the stapes and reduces its mobility. If this condition of immobility is continued for many years, there is an impairment of the blood supply to the ear and other changes that finally lead to otosclerosis.

To test this assumption the static pressure in the vestibular organ was altered by injecting water by means of a hypodermic needle with a weight on the piston of the syringe (see Fig. 11-30). By rotating the piston continuously with special equipment it was possible to reduce the friction in the glass tube so that the pressure in the fluid could be calculated from the weight.

A measurement was first made of the maximum static pressure that the inner ear could bear. It was found that at a pressure of about 4 atm a faint click was heard in the temporal bone, and after this the bone began to drip. Probably one of its blood vessels had burst. Special prepara-

tions of the round window showed that the round window ruptured at static pressures of from 4 to 7 atm. The stapes was not visibly affected by the maximal pressures that could be produced in the cochlea. The force necessary to tear it out by means of a hook was about 320 grams, which corresponds to a pressure of 16 atm applied to the footplate.

After these preliminary measurements on several very fresh temporal bones the volume displacement of the round window was measured for 300 and 1000 cps by adjusting the current in the earphone (see Fig. 11-30) so that the tone in the ear of the observer was minimal. This adjustment was so precise that the smallest change in phase or amplitude of vibration of the round window could easily be detected. In general, no changes were observed as the internal pressure in the cochlea was continuously increased until just before the inner ear started to drip. Then there was a change in amplitude of about 10 to 20 per cent. From these observations it appears that an increase of the pressure in the inner ear probably does not immobilize the footplate of the stapes.

As shown in Fig. 11-31, the volume displacement of the round-window membrane and of the fluid of the cochlea are practically independent of frequency. To discover which parts of the ear contributed significantly to this function, measurements were made of the amplitude of vibration of the fluid in the cochlea on the successive removal of the eardrum, ossicles, stapes, and round-window membrane. In a second set of measurements, made through the internal meatus, the movements of the round-window membrane and the stapes were also studied (see page 96).

In preparing for measurements of the movements of the cochlear fluid, it is important that none of the fluid be lost when the round-window membrane is removed and the stapes is torn out. Similarly, it is necessary that the openings in the cochlea be so positioned that no fluid can escape. The viscosity coefficient of the perilymph in living man at a temperature of about 37°C is 30 to 50 per cent less than at a room temperature of 20°C. In order to estimate the error caused by this temperature difference, the cochlea was filled with a solution of glycerin and water with a frictional coefficient of 0.02 cgs at 20°C, which corresponds to the value for perilymph at 37°C (see page 406). The measurements showed that the mobility of the fluid in the cochlea was not appreciably changed by substituting the water-glycerin mixture for the perilymph. It was also shown that there was no change when the fluid in the cochlea reached the rim of the cement wall around the round window. As the diameter of the opening was larger than that of the body of the cochlear canal, it follows that the capillary forces on the surface of the perilymph did not influence the mobility appreciably.

The ratio of the volume displacement of the perilymph to the pressure difference between the two windows of the cochlea is shown in the lower curve of Fig. 11-32. Both the stapes and the round window have been removed. The upper curve shows the phase angle between the volume displacement and the pressure difference. For lower frequencies the impedance of the perilymph alone is a resistance, but for the higher

frequencies, those above 1000 cps, the effect of inertia is the greater. According to Poiseuille's law of friction, the frictional loss (force) in a capillary tube is proportional to the fourth power of the radius of the tube. In the canals of the cochlea the cross-sectional area is, in general, larger than 1.2 sq mm, except near the round window, where the area is 0.6 sq mm. However, the cross-sectional area of the helicotrema is only about 0.4 sq mm, and for very low frequencies the frictional loss is apparently caused entirely by the streaming of the perilymph through the helicotrema.

When fluid was made to flow continuously through the cochlea and the amount passing through in a given time was measured for a constant pressure difference between oval and round windows, it was found that the streaming resistance of the cochlea is equal to that of a capillary tube

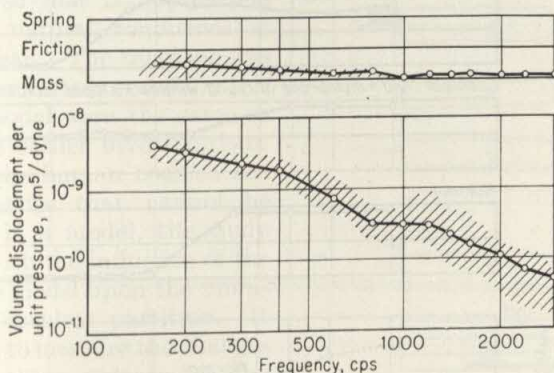


FIG. 11-32. Volume displacement of the cochlear fluid when the stapes and round-window membrane were removed. The upper curve shows the phase angle and the lower curve the amount of displacement per unit of pressure.

6 cm long with an inside diameter of 0.69 mm. For a fluid with a frictional coefficient of 0.02 cgs and with a pressure difference between the two windows of 1 dyne per sq cm, the amount of fluid running through the cochlea per second is $V = 5 \times 10^{-6}$ cu cm.

The measurements of the mobility of the perilymph alone showed little variability, but other parts of the cochlea sometimes showed large individual differences. For instance, the volume elasticity $\Delta V/p$ of the membrane of the round window varied between 10^{-9} and 10^{-10} cu cm per dyne per sq cm. These differences were obvious from the wide variations in the surface of the round-window membrane. The varying thicknesses of the membrane are correlated with changes in transparency. The mobility of the stapes showed large changes too. Sometimes the impedance was practically a friction, and sometimes it was a pure elasticity.

In general, one of two situations was found: either the round window was stiff and the stapes was mobile or the round window was very yielding and the stapes relatively immobile. Obviously it is irrelevant for hearing, especially for low frequencies, whether the mobility of the fluid in the cochlea is determined by the elasticity of the round-window

membrane or of the stapes. To obtain a better picture of the impedance of the different parts of the cochlea, one part after another was removed, and the movements of the perilymph were measured. The results are shown in Fig. 11-33 for an ear with a yielding round window. The upper curve shows the phase angle between the volume displacement and the pressure difference for the perilymph, in the absence of both stapes and round-window membrane. For the higher frequencies, the phase angle corresponds to that of a mass, and for lower frequencies it approaches

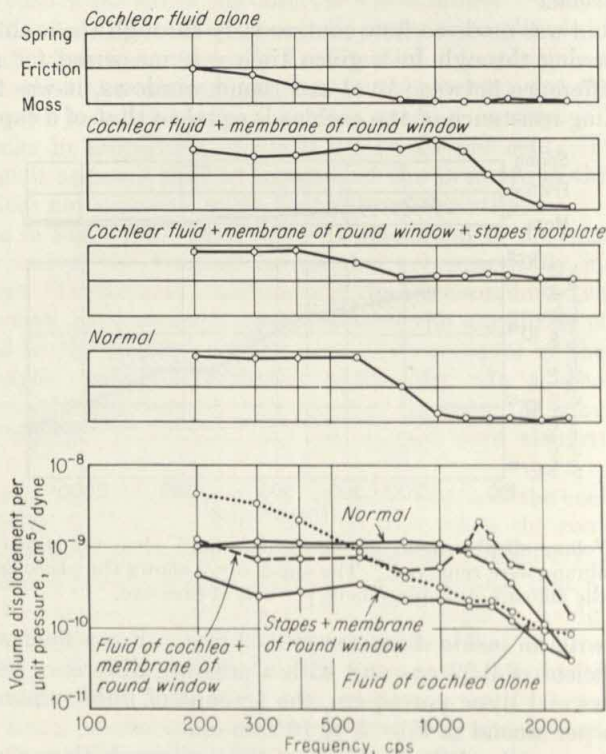


FIG. 11-33. Phase angle and volume displacement of the round-window membrane after removal of various structures as indicated.

the characteristics of a system having only friction. If the membrane of the round window is not destroyed, the vibrating system, consisting of the round-window membrane and the perilymph, shows a resonant peak near 1400 cps, as seen in the second curve of Fig. 11-33. If the stapes footplate, the round window, and the perilymph are intact, the whole system behaves like an elasticity with frictional losses predominant at higher frequencies, as evidenced by the third curve of Fig. 11-33. For the normal ear with eardrum and ossicles intact, the resonant frequency is around 800 cps (fourth curve).

The lower set of curves gives $\Delta V/p$ for the various stages of simplification. From these curves we may draw the same conclusions as from the

curves that show the dependence of the phase angle on frequency. Further, it is possible to see from the lower curves that when the eardrum is intact there is an appreciable pressure transformation. Consequently the volume displacement of the perilymph is larger than when there is an eardrum. This effect is especially marked below 1000 cps.

Experiments with a Model of the Cochlea. To complete the investigation of the vibrations in the cochlea a model of the inner ear was used that had been constructed earlier (page 405). Inasmuch as measurements were now available of the elastic properties of the cochlear partition, this model was again of interest. It was possible to adapt the model so that it approached closely the natural conditions in the human ear. The question was whether the effects observed in this improved model were the same as those in the earlier investigations.

Because the human cochlea has some properties that cannot be reproduced in a model, the study dealt first with the influence of the shape of the model upon the vibrations of the cochlear partition. It was possible to measure the changes in the vibratory pattern of the membrane exactly, because, as shown previously and also in the upper drawing of Fig. 11-34, two eddies occurred during the vibration of the membrane. These eddies changed their positions if the membrane changed its pattern of vibration. If the frequency of the vibration of the stapes was raised, the eddies approached the stapes; and if the frequency was lowered, the eddies moved toward the helicotrema.

The cochlear model was constructed by cutting a broad slot from end to end in a 1.2 mm square brass rod, leaving intact the top and bottom and two ends. Two openings were bored through the left end. These openings were covered with a stretched rubber membrane, and to one of these membranes a short metal rod was attached to represent the stapes. The cavity in the metal frame was bisected lengthwise by a second, smaller metal frame covered by a rubber membrane. The open sides of the first frame were covered with glass plates, and the whole model was filled with water.

It was found that changes outside the frame near the stapedial foot-

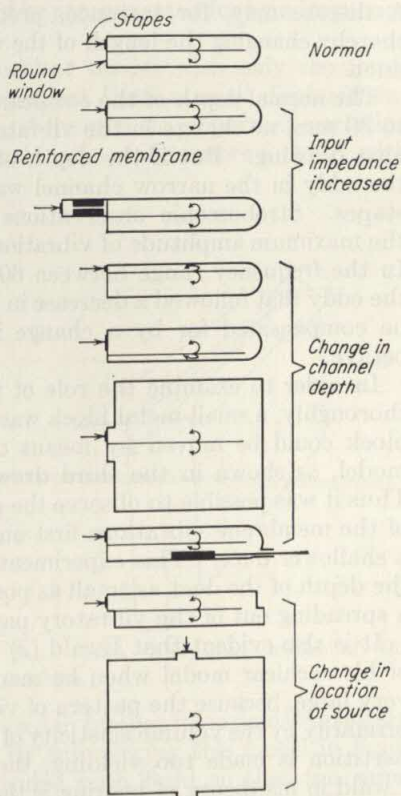


FIG. 11-34. Models with various modifications of form, as indicated.

plate and the round window did not affect the vibratory pattern of the rubber membrane when it was observed stroboscopically. Specifically, neither a change in the elasticity of the membrane over the round window nor a change in the length of the cochlear canals affected the vibratory pattern (see Fig. 11-34). This seems important from the physical point of view, because it implies that frequency discrimination in the cochlea is not altered by a change in the middle ear caused by disease. A disease may, for instance, produce a secretion in the middle ear, thereby changing the length of the vibrating fluid column in the cochlear duct.

The normal depth of the cochlear duct is 1 mm. If this was increased to 30 mm, no change in the vibratory pattern occurred, as shown in the next drawing. But if the depth of the duct was decreased to 0.3 mm, the eddy in the narrow channel was broadened and moved toward the stapes. Stroboscopic observations indicated clearly that the place of the maximum amplitude of vibration moved in the direction of the stapes. In the frequency range between 600 and 2400 cps, the displacement of the eddy that followed a decrease in the depth of the duct to 0.3 mm could be compensated for by a change in the frequency of one-half to one octave.

In order to examine the role of the depth of the cochlear duct more thoroughly, a small metal block was inserted into one of the ducts. This block could be moved by means of a rod with its handle outside the model, as shown in the third drawing from the bottom of Fig. 11-34. Thus it was possible to observe the position of the eddies and the pattern of the membrane vibrations first under normal conditions and then with a shallower duct. This experiment made it clear that nature has made the depth of the duct as small as possible without going so far as to cause a spreading out of the vibratory pattern along the cochlear partition.

It is also evident that Ewald (2) made no mistake in the construction of his cochlear model when he made the depth and width of the canal very large, because the pattern of vibration of the membrane is governed primarily by the volume elasticity of the membrane itself. If the cochlear partition is made too yielding, the vibratory pattern conceived of by Ewald in his theory of hearing is the result. The two lower drawings in Fig. 11-34 indicate that the locus of the eddy is unaffected by moving the stapes to various positions.

In all these experiments the length of the column of fluid in the model was the same as in the normal ear, namely, 35 mm, and the elastic properties of the membrane were matched as closely as possible to the elastic properties of the human cochlear partition.

The surprising stability of the pattern of vibration along the membrane is shown by the experiments illustrated in Fig. 11-35. If the fluid was removed from one of the channels, then the eddy moved toward the stapes, but the displacement was small, and by lowering the frequency 15 to 25 per cent the eddy could be brought back to its former position. In the model in which only one channel was filled, it was immaterial whether the fluid was moved by vibrations of the stapes, as is normally

the case, or by leading air-borne sound to the empty canal, which would produce a sound pressure equal in magnitude along the whole cochlear partition. The second drawing from the bottom in Fig. 11-35 shows that the place of the eddy and the vibratory pattern of the membrane were still maintained, even if a third of the remaining fluid was removed.

Increasing the coefficient of friction of the fluid in the model by a factor of 10, by putting some honey in the water, caused the eddy to move toward the stapes. This change could be compensated for by a frequency change of one-half octave.

Stroboscopic observations of a cochlear model with only the lower channel filled with fluid showed that, apart from a small displacement of the locus of maximum amplitude, there was no important variation from the vibratory pattern of a normal model. Therefore a model with

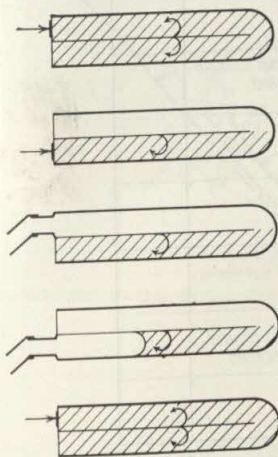


FIG. 11-35. Effects of removing fluid from one channel of the model.

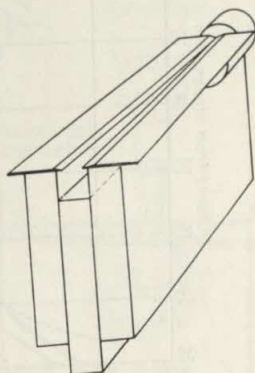


FIG. 11-36. Simplified model of the cochlea.

only one channel filled with fluid was used in further investigations simply because it was easier to construct. By submerging this model in fluid, both sides of the membrane were loaded with fluid so that the same properties were obtained as in the normal model. The difference between a one-channel model and a two-channel model has been investigated mathematically by Ranke (1).

The simplified model is illustrated in Fig. 11-36. It was made of three microscope slides 1 mm thick so arranged as to produce, at the top, a trough with a cross-sectional area of 1 sq mm. On the top of the outer two glass plates two thin metal strips (razor blades) were attached to the end of the trough and closed with a rubber membrane. To this rubber membrane a small piston was fastened to represent the stapes.

With a small wire loop, a drop of rubber solution was drawn over the metal strips, forming a thin membrane between them. The loop was moved by a mechanical device at a controlled velocity so as to ensure uniformity of the rubber film. The process was adjusted so that the

membrane had a thickness, after drying, that gave it the same volume elasticity as the basilar membrane at every point. Because the model is simple it is not difficult to approximate closely the conditions of the natural cochlea.

For this model the location of the middle of the eddy was measured for different frequencies. In Fig. 11-37 the ordinate represents the distance of the middle of the eddy from the narrow end of the membrane. To compensate for the small differences between the volume elasticity (pages 474 and 476) of the actual ear and that of the model arising from variations in the rubber film, a number of models were constructed, and the measurements obtained from them were averaged. This average is represented by the thin solid line of Fig. 11-37. This curve differs

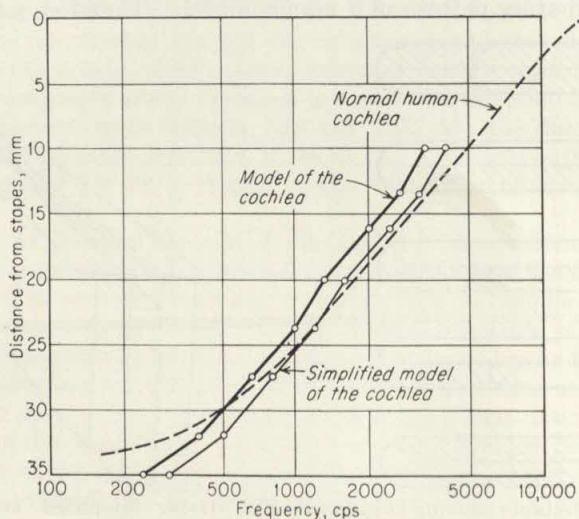


FIG. 11-37. Place of maximum stimulation as a function of frequency in the normal human ear, in a complete model, and in a simplified model.

but little from the one obtained with two canals, as shown by the heavy line; in fact, one curve can be transformed into the other by moving it along the frequency scale by about 20 per cent.

Observations made on the model showed that the mid-point of the eddy represented precisely the place of maximum amplitude of vibration of the membrane. Also it was possible to relate the locus of destruction in the actual cochlear partition to corresponding hearing losses. In this way a comparison was made of the location of maximum movement of the basilar membrane for a given frequency in the model of the ear with the location in the natural ear for the same frequency. Stevens and Davis summarized the available observations for the human cochlea up to 1938 in a curve whose values are represented by the broken line in Fig. 11-37. Considering the difficulty of the measurements and the different methods by which the results were obtained, the agreement between the curves is remarkable. Consequently, the experiments done

on the models seem to be justified. Normal conditions were approached even more closely by placing a thin layer of gelatin on the rubber membrane to represent the cochlear duct.

Place of Maximum Vibration in the Human Cochlea. Not only in the model, but even in a fresh preparation, it was possible with the technique used to observe the vibratory pattern of the cochlear partition for the different frequencies. For this purpose the middle ear, including the membrane of the round window and the stapes, was removed. To the rim of the round window a short brass tube was fastened with dental cement. Over this first tube a second brass tube, provided with a rubber membrane, was tightly fitted. After these preliminary preparations, the temporal bone was put under water, and the tip of the cochlea was ground away so that one turn of the cochlear partition was visible. It

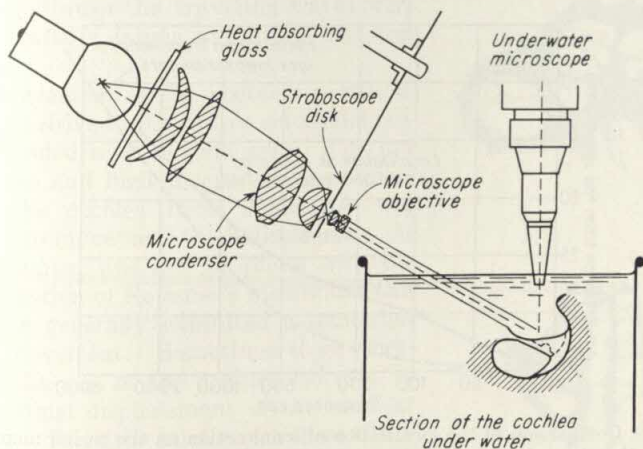


FIG. 11-38. Method of illuminating the cochlea with a stroboscope.

was important to be sure that no air bubble remained in the cochlea after the preparation had been completed. This was assured by allowing fluid to stream through the cochlear canals. After this the tight-fitting tube with the rubber membrane was placed in position, and a small metal peg, representing the stapes, was attached to the rubber membrane. This block was connected with an electrodynamic driving system. After observations were made on the vibratory pattern of the exposed turn of the cochlea, the grinding was carried farther so that the parts of the basilar membrane closer to the stapes could be studied.

In order to measure the place of maximum vibration, stroboscopic illumination was used, and to make the transparent Reissner's membrane visible some silver crystals were dropped on the membrane. For the stroboscopic illumination a small projector with heat-absorbing filters was used. With the help of a microscopic condenser lens the light was concentrated so that, in the plane of the perforated stroboscopic disk, an image of the incandescent lamp of about 0.1 mm was produced. As shown in Fig. 11-38, the light rays going through the stroboscopic disk

were collected by the objective of the same microscope and were made practically parallel.

In preliminary measurements the optimal amplitude of the electrodynamic vibrating system was determined so that no overloading of the basilar membrane occurred. After the place of maximum amplitude on the basilar membrane was determined for a given frequency, this place was located on a map of the cochlear partition (see page 29).

The distance between the place of the maximum amplitude of vibration and the footplate of the stapes for the different frequencies is given in Fig. 11-39. Above 3000 cps it was no longer possible, with the technique described, to measure exactly the location of this maximum, because the movement of the basilar membrane was not transmitted to Reissner's membrane with the same vibratory pattern, and observations of the

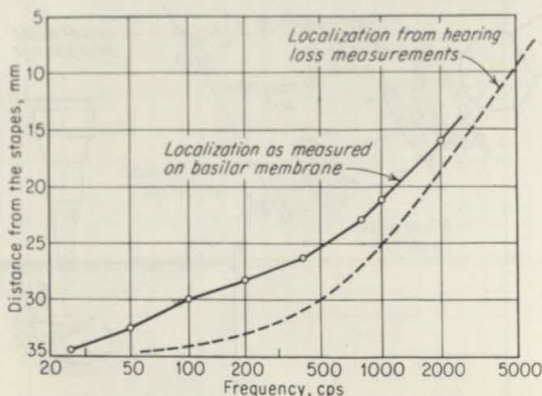


FIG. 11-39. Comparison of the localization of tonal action on the basilar membrane as observed directly and as derived from measurements of hearing loss.

basilar membrane itself were no longer possible through the cochlear duct. Measurements in this part of the curve require a preparation in which the cochlear duct is seen, not from the side of Reissner's membrane, but from the side of the basilar membrane.

It was surprising that displacements of the pattern of vibration were found for frequencies as low as 25 cps. Under the microscope a difference between the vibratory patterns for a tone of 20 cps and a tone of 40 cps could easily be recognized. In the model, the displacement of the maximum usually could not be observed below 200 cps because the whole membrane of the model vibrated in the same phase. One reason for this discrepancy is that the volume elasticity at the edge of the helicotrema was not as great in the rubber membrane as in the normal ear simply because in the process of spreading the rubber solution between the metal strips capillary forces caused a drop of the fluid to remain at the end of the opening. Also the helicotrema in the model was different from the helicotrema in the normal ear. In the normal ear a length of about 7 to 8 mm of the cochlear partition surrounds the helicotrema. In the model

this could be reproduced only by winding the membrane around the helicotrema, and it is difficult to construct a smooth rubber membrane for a round channel.

In removing the stapedial footplate great care was taken that there should be no mechanical overloading of the cochlear partition so that the whole of Reissner's membrane might continue to act as a part of the cochlear partition. When this was true, the displacement of the partition for frequencies below 3000 cps showed no phase difference between the movement of Reissner's membrane and that of the basilar membrane. The traveling waves in the model caused by a click were easily observed, but in the normal ear they are more quickly absorbed by the viscous fluid in the cochlear duct. When the gelatinous mass of the cochlear duct was removed from the basilar membrane with a fine brush the traveling waves were observed with a larger amplitude and less damping.

The movement of the cochlear partition, even when driven with simple sinusoidal motion, extended over a wide area. For low frequencies and high intensities the central axis of the cochlea itself sometimes was observed to move near the helicotrema. As this movement was not in phase with the usual vibration of Reissner's membrane, this membrane generally exhibited a somewhat circular movement. Sometimes these vibrations of the axis of the cochlea led even to a longitudinal displacement of the cochlear partition. From the existence of these vibrations of the axis of the cochlea we must conclude that the degree of mechanical isolation between the two cochlear canals lying one above the other has no influence upon hearing. From cross sections of the human cochlea

shown in Fig. 11-40 we can see that, as might be expected, the wall between the two scalae lying one above the other is thicker near the base. But in the cochlea of a guinea pig, which is surely highly developed, the thickness of this wall does not vary. Even in man the wall is sometimes so thin that it can be broken instantly merely by touching it with forceps. According to the lower drawing in Fig. 11-34 the type of transmission of vibration to the fluid in the cochlea makes no difference in the vibratory pattern of the cochlear partition.

Simplified Representation of the Vibrations in the Cochlear Partition.

For a mathematical treatment of the vibrations of the cochlear partition it is important that the observed vibratory pattern be simplified. In the history of the physiology of hearing three types of simplification can be distinguished.

In one class of theories, represented especially by Lux and Roaf, there



FIG. 11-40. Cross sections of the cochlea of man and a guinea pig.

is a strict separation between the elastic forces in the cochlear partition and the forces derived from the mass of the vibrating fluid column. Therefore, their theory is based on simple resonant systems. As shown in the upper drawing of Fig. 11-41, the mass in the resonant system will be given by the length of the vibrating fluid column, and the elasticity by the stiffness of the cochlear partition at the place of maximum vibration. In the second type of theory, it is assumed that the cochlear partition itself constitutes a series of resonators, and the mass of the fluid in the neighborhood will act only to lower the natural frequencies of these resonators. The resonance theories postulated by Du Verney and Helmholtz belong to this group. In the third type of theory the hydrodynamic problems are taken into consideration, and the cochlear partition plays only the role of a membrane with a known volume elasticity.

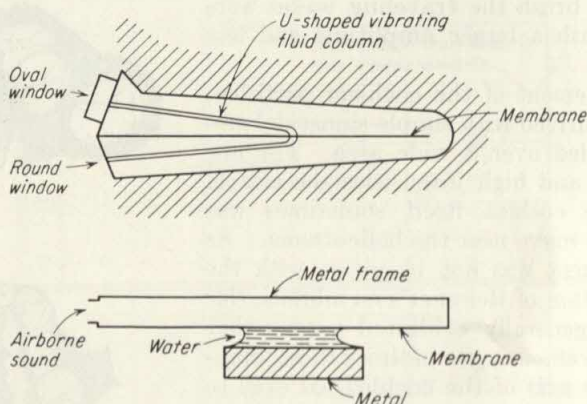


FIG. 11-41. Method of studying the effects of the length of the fluid column. In the lower drawing the fluid column has been reduced to about 0.5 cm near the region of maximum vibration.

It is possible to classify these three types of representation as the U-tube type, the vibrating-plate type, and the hydrodynamic type.

These three representations are simplifications in three different directions. In general they are sharply delineated one from the other. It was therefore most valuable that in the calculations of Ranke (3) the last two theories for the first time were reconciled.

The following experiments were undertaken in the attempt to determine which of the simplifications described above comes closest to natural conditions. First of all it is necessary to point out that the U-shaped movements of the fluid in the cochlea can approach the natural situation only in the lower frequency range. To prove this the fluid was removed from the simplified model of the cochlea (Fig. 11-36), the helicotrema was closed, and air-borne sound was introduced through the oval window into the enclosed channel. Then it was possible to see the entire length of the membrane vibrating in the same phase. But if the membrane was brought into contact with a long drop of fluid, the vibratory pattern of this part of the membrane became the same as under normal conditions,

provided, of course, that the rubber membrane in the model had been adjusted to match the elastic properties of the normal cochlear partition. In this experiment the drop of fluid did not represent a vibrating fluid column. Consequently the U type of vibration cannot be very important. This experiment shows that it is not even necessary for the fluid surrounding the membrane to be enclosed in a tube, for in the middle frequency range only the fluid close to the cochlear membrane influences the vibratory pattern of the membrane.

To simplify the calculation of the hydrodynamic problem, a study was made to determine whether or not the eddies are important in the vibratory pattern of the membrane. If a suppression of the eddies does not change the vibratory pattern, then it is possible to calculate the pattern of the membrane without taking into consideration the hydrodynamic rectification effects that produce the eddies. To retard the flow of the fluid in the cochlea the lower channel of the model (Fig. 11-42) was filled with warm gelatin solution, and observations were made of the eddy in the upper channel and the vibratory pattern of the membrane under stroboscopic illumination. As the gelatinous mass gradually cooled and congealed no important changes were observed in the eddy and the vibratory pattern of the membrane. The gelatinous solution was made by allowing dry gelatin to stand in water overnight and then pouring off any water that had not been absorbed. The saturated gelatin was warmed in a steam bath. This mass was so soft that, after congealing, the volume elasticity of the cochlear partition in the model was not changed. It was even possible to place a simplified model on a soft, congealed gelatin block, as shown in Fig. 11-42, without changing the position of the eddy in the model. An attempt was made to use the lower lip, instead of the gelatin block, to produce a model of the inner ear with nerve endings. However, these experiments were unsuccessful because, unlike the basilar membrane, the vibrations from the model were felt not only on the surface of the lips but even in the deeper-lying tissues. The smallest displacement of a vibrating body that can be recognized on the surface of the lip is about 1 cm. Consequently the place discrimination for the different frequencies was not pronounced enough to permit a comparison with the ear.

The channel between Reissner's membrane and the basilar membrane was filled with a soft mass. In order to investigate the influence of this mass on the rubber membrane of the model in Fig. 11-36, a soft gelatinous

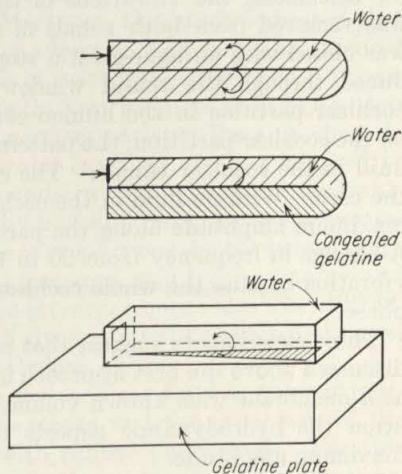


FIG. 11-42. Method of preventing the formation of eddies.

layer 0.2 to 0.5 mm thick was spread on the membrane. In this case the place of maximum amplitude moved toward the stapes. The maximum displacement could be compensated for by a frequency change of half an octave. The waves traveling toward the helicotrema were damped, and the wavelength was doubled.

The mathematical treatment would be simplified if the cochlear partition could be conceived of as an elastic plate. The relatively large mass of the cochlear duct makes it possible that the mass of the fluid loading the membrane could be calculated by a progressive approach. The vibratory pattern would first be calculated for the membrane without fluid in the canals, and after this the change in the vibratory pattern caused by the load of the fluid could be estimated and added in. It is unfortunate that this simplified mathematical approach is not possible for calculating the vibrations of the cochlea. To prove this the fluid was removed from both canals of a human cochlea. The helicotrema was closed with an agar-gelatin stopper, and air-borne sound was introduced through the round window. If the vibratory pattern of the cochlear partition in the human ear were independent of the fluid load on the cochlear partition, the pattern would be the same with and without fluid in the cochlear canals. The experiment showed that this was not the case. With no fluid in the cochlea there was no displacement of the maximum amplitude along the partition as the frequency was changed. A change in frequency from 20 to 1000 cps did not alter the pattern of vibration because the whole cochlear partition was vibrating in the same phase.

These experiments suggest that of the three methods of simplification discussed above the best approach is to conceive of the cochlear partition as a membrane with known volume elasticity and to take into consideration the hydrodynamic aspects of the vibrations near the place of maximum amplitude.

RESONANCE AND DECAY PROCESSES IN THE COCHLEAR PARTITION*

The anatomy of the cochlea is such that vibrations of various frequencies transmitted from the stapes are in some degree distributed spatially along the cochlear partition. Now to be considered is the extent to which the amplitude of vibration of the partition exhibits a spatial separation for the different frequencies, and what decay times are associated with this mechanical analysis of frequency.

Distribution of Amplitudes along the Cochlear Partition for Different Frequencies. In order to study the propagation of sinusoidal vibrations along the cochlear partition, the dome of the cochlea was ground off under water, and the opening was sealed again with a microscopic cover glass. This operation exposed one turn of the cochlea and permitted measurement, under stroboscopic illumination, of the vibrations of this section of the partition. The vibrations were measured under a binocular

* Article 43 as listed in the Author's Bibliography. Published in 1943.

microscope with a magnification of seventy-two times. The most difficult part of the operation was attaching the glass window under water.

In earlier experiments with a model it was demonstrated that the form of vibration in the cochlear partition is not altered essentially if the cochlea is opened at the helicotrema, so that the vibrations of the stapes are transmitted only to the column of fluid between the stapes and the helicotrema (page 437). It seemed unnecessary, therefore, to seal the openings produced in the preparations. However, control measurements were always made on preparations with these openings sealed so that any small changes in the vibratory pattern caused by the opening in the cochlea could be observed.

Because the cochlea was opened under water, the glass window had to be attached under water also to prevent air bubbles. A study of the literature on adhesives (Micksch, C. Breuer, Lehner) failed to disclose any substance usable under water. Moreover, this study indicated that the chemical and physical problems of adhesives had not been explored scientifically. Therefore a long series of tests was undertaken. It was found that the dental cements, such as De Trey's copper precipitate, that are used especially for children and nervous patients (because they do not require complete drying of the dental cavities) are best adapted to joining glass and metal to fresh bone under water. The most favorable of these cements are determined only by trial and error, for the properties can be completely altered by the choice of proportions, by the temperature of the surface on which the mixture is prepared, and by the manner and speed of the compounding. A litharge-glycerin cement also was utilized. It consisted of fired litharge mixed with glycerin (that had been desiccated at 80° for 24 hr) and a few drops of ethylene glycol.

In order to transmit vibrations to the cochlear fluid in these experiments, it was expedient to remove the stapes and the membrane of the round window and to replace them with rubber membranes. For this purpose a small brass ring was cemented to the protruding bony structures surrounding the windows, and over this ring was slipped a second ring across which a rubber membrane had been stretched. The vibrations from the driving unit of a loudspeaker were transmitted to one of the membranes by a knob (artificial stapes) attached to the rubber membrane.

The vibrations observable through the microscope were relatively large, and the next step was to discover whether nonlinear distortions appeared in the measured amplitudes. The data showed that the amplitude of vibration of the cochlear partition, as observed at a particular point, increased exactly in proportion to the amplitude of vibration of the loudspeaker system, so that no distortion was present.

At frequencies below approximately 30 cps, the whole cochlear partition near the helicotrema vibrated with almost the same amplitude. As the frequency was raised, however, the vibrations moved away from the helicotrema until, at frequencies above 800 cps, no further vibrations could be seen in the exposed spiral. The measured amplitudes of vibration, expressed in volume displacement per millimeter of length of the partition, constitute the ordinate in Fig. 11-43. This scale is

arbitrary for each individual frequency. The abscissa represents the distance from the stapes to the measured point. The distances were determined by noting the direction of the cochlear duct and converting the angle into distance by means of a chart of the cochlea, as described on page 29.

Because the uppermost turn of the spiral was only 8 mm long, the technique of preparation described above permitted study of only those vibrations that occurred 27 to 35 mm away from the stapes. In order to study the vibrations nearer the stapes, it was necessary to grind away more of the upper end of the cochlea. As shown in Fig. 11-43, this upper section of the cochlear partition does not vibrate at frequencies above 800 cps. Shortening the partition, therefore, did not alter the conditions of vibration when the cochlea was being driven at these higher frequencies. Consequently, it was possible to measure the amplitudes at different distances from the stapes, even though only one turn could be observed at a time. Although the amplitudes fell off relatively sharply on the side toward the helicotrema, it was nevertheless possible to observe a fairly complete range of amplitudes in the one turn open to view. The amplitudes were measured from millimeter to millimeter along the partition, and the values obtained in this way are represented by the solid curves in Fig. 11-43.

In order to determine how the amplitude falls off on the side toward the stapes, the vibrations of the artificial stapes were held at a constant amplitude while more and more was cut away from the cochlear apex,

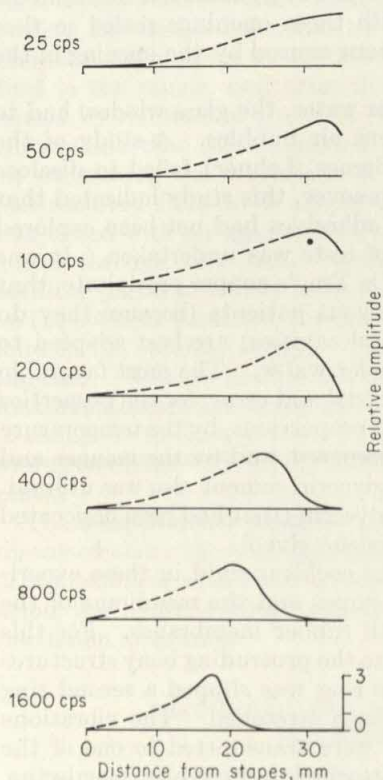


FIG. 11-43. Patterns of vibration of the cochlear partition of a cadaver specimen for various frequencies.

until finally the lowest turn was visible. The measurements of amplitudes obtained at this point, represented in Fig. 11-43 by broken lines, were no longer exact because the upper end of the partition had meanwhile been destroyed, and because at frequencies below approximately 100 cps the fluid no longer had to flow along the whole length of the cochlear partition. This situation is illustrated in Fig. 11-44. With constant volume displacements of the artificial stapes, the pressure difference between the two scalae of the cochlea was decreased, and therefore with the amplitudes of movement of the partition decreased as well.

However, if care was taken to maintain as great a distance as possible between the measured point and the destroyed section of the cochlear partition, *i.e.*, if the distance was as much as the length of a full turn, the resulting error was small. This is confirmed by the fact that experiments with the model produced the same distribution of amplitudes as shown in Fig. 11-43.

It was of fundamental importance to measure vibrations in that section of the partition adjoining the stapes without destroying the cochlea. A method was therefore devised to open the cochlea at the base instead of at the apex. This method of preparation was much more difficult than opening the cochlea at the apex because more bone had to be removed. The helicotrema could be seen through the remaining layer of bone after only a few tenths of a millimeter had been cut away at the apex, whereas several millimeters had to be removed if the cochlea was opened from the medial side (toward the brain). With a cochlea from the right ear the best procedure was to hold the medial surface of the

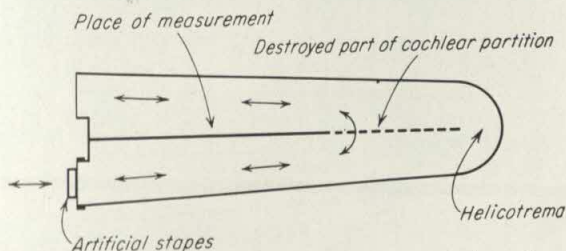


FIG. 11-44. Effects on fluid movement of destroying the apical portion of the cochlea.

petrous bone horizontal, as in Fig. 11-45, and after removing the superfluous bony parts to fasten it in this position into a metal ring by means of gypsum. This ring, described elsewhere (page 27), could then be screwed into an apparatus designed for preparing specimens under water. The remainder of the procedure consisted in removing thin horizontal layers of bone along the auditory nerve by means of a diamond grinding wheel or a finishing burr such as dentists use. This process continued until the cochlear duct winding around the auditory nerve was visible through the bone. At this stage, the further steps in opening the lumen could be taken with complete safety. In cutting away different layers, it was found expedient to start with the grinding from the auditory nerve and to move in a radial direction from the center to the periphery. This was the quickest way to reach the stage at which the cochlear lumen was dimly visible through the bone. With the positive orientation established, it was safe to use coarser tools on the surrounding bony structure.

When the position of the petrous bone was that shown in Fig. 11-45, the grinding could not be carried from the auditory nerve toward the left because of the danger of opening the semicircular canals. Since the semicircular canals are directly connected with the vestibule, the result of opening them would be that a movement of the stapes would produce

a displacement of the fluid in the semicircular canals instead of in the cochlea.

Figure 11-46 shows a cochlear spiral opened from the base in the manner described above. The modiolus (cochlear axis) is in the center of the spiral. Because the modiolus supports the upper spirals of the cochlear partition, it was necessary to preserve a bridge of bone to keep this center firmly in place. Any grinding on this bridge of bone had to be done with care because the vibrations of the drill were transmitted to the axis, thus tearing the cochlear partition. Special care had to be taken also to retain the bony wall on the peripheral part of the cochlear



FIG. 11-45. Position of the temporal bone when the cochlea is opened at the basal end.

partition for at least half a millimeter above the cochlear partition. This was because the spiral ligament, to which the basilar membrane is anchored, rises about half a millimeter above the level of the partition. If this anchorage were loosened, the elasticity of the cochlear partition would be altered.

It sometimes happened that, despite all precautions, the preparation of a cochlea from the side of the auditory nerve was unsuccessful. Then if vibrations of various frequencies were led to the stapes, the form of vibration along the basilar membrane would exhibit hardly any changes. The chief phenomenon was a resonance in the region of 400 to 800 cps, which masked the normal vibratory pattern of the partition. This disturbing resonance was probably due to the semicircular canals. The blood vessels supplying the canals had been opened when sections of bone were cut away, so that the canals were not sealed off from the out-

side as completely as in life. This interpretation was supported by the fact that the disturbing resonances were eliminated by cutting away the semicircular canals and sealing the openings leading to the stapes.

By this procedure it was possible to measure the amplitudes of vibration near the stapes and to verify the dotted section of the curves of Fig. 11-43.

The appearance of disturbing resonances and the difficulty with which they were avoided—only by a painstaking cementing of openings leading

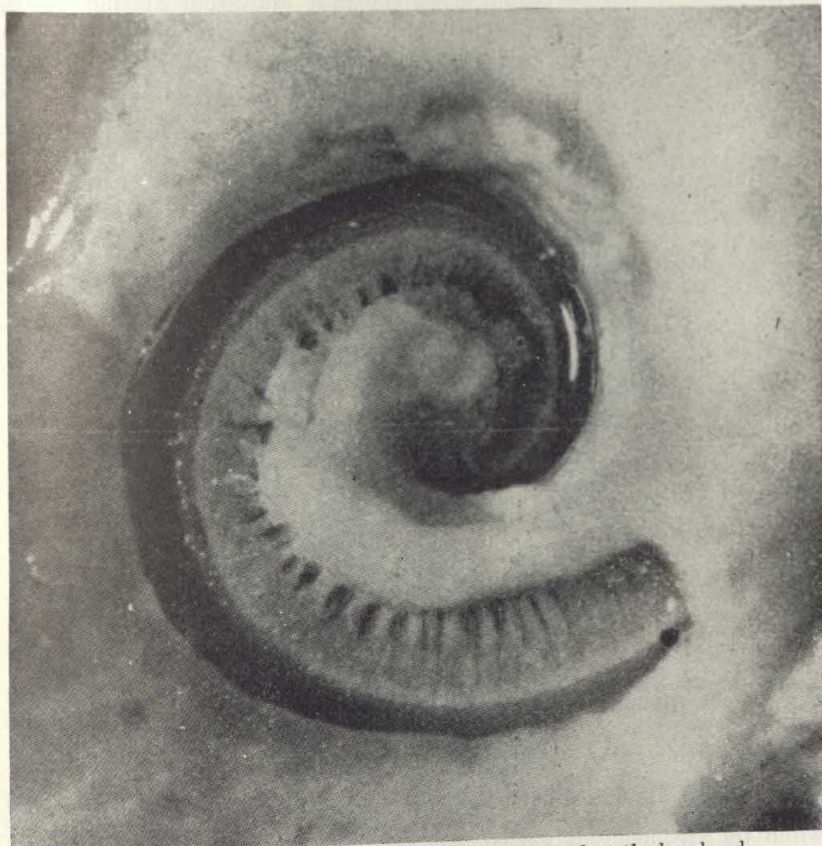


FIG. 11-46. View of the cochlear spiral when opened at the basal end.

to the semicircular canals—raised the following question. Why is the natural stapes located on that side of the cochlear partition that leads to the semicircular canals? Figure 11-47 illustrates how much more expedient it would be, from the physical standpoint, if the stapes were attached at the round window. Then the sound pressure would be exerted only on the cochlear partition, and its vibrations would not be affected by an increase in compliance at some point in the complicated structure of the semicircular canals and other adjoining organs. The

answer is probably that, at some earlier stage in the evolution of the vertebrate ear, or even at the present stage, vibrations of the stapes under certain conditions could stimulate the organs near the semicircular canals.

Transmission of Vibrations from the Stapes to Various Points on the Cochlear Partition. The distribution of amplitudes of vibration along the cochlear partition for various frequencies has already been established. The next step is to determine how the amplitude of vibration varies at a given point on the partition, given constant amplitude at the stapes, given constant amplitude at the stapes,

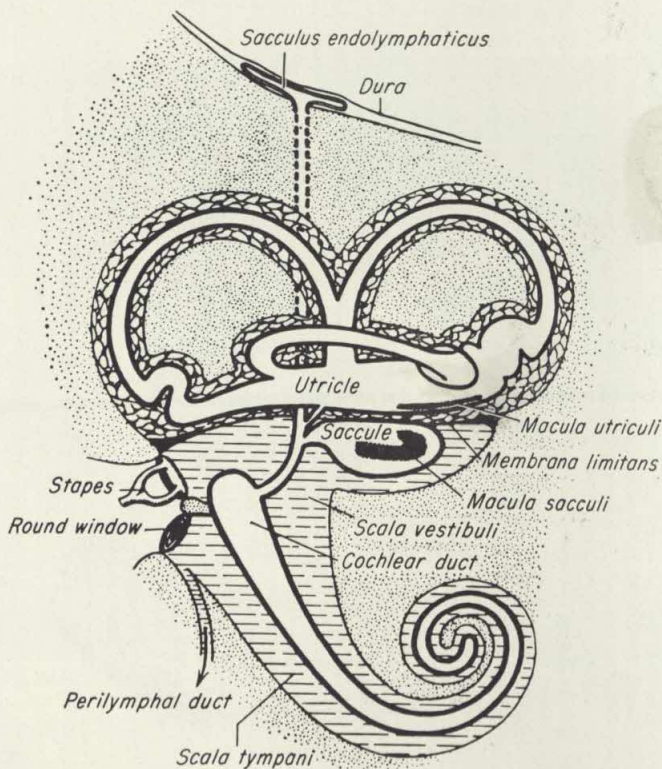


FIG. 11-47. Schematic drawing of the labyrinth, after de Burlet.

when the frequency is varied over the entire auditory range. Figure 11-48 illustrates the apparatus designed for these measurements.

The lower part of the figure shows, in cross section, the petrous bone opened at the cochlear apex. It was fastened with gypsum inside a brass ring, which could be screwed either into the apparatus used in the surgical preparation or into that designed for measurements. This permitted rapid preparation without undue disturbance of the specimen. The petrous bone was immersed in water, and small crystals of silver were scattered on the cochlear partition to make it more clearly visible. Observations were made through a microscope with a water-immersion

objective of approximately seven times enlargement (a plankton objective). Possible vibrations on the surface of the water were thus eliminated as a disrupting factor, and also the lens could be placed diagonal to the water's surface without affecting the focus. The total magnification amounted to 126 times. A small tube *R* was fastened into the round window after removal of its membrane; a second small tube, equipped with a ring across which a rubber membrane had been stretched, fitted over *R* and served to transmit vibrations to the specimen. A little knob, which had already been fastened to the rubber membrane with adhesive wax, protruded partly out of the water. This protruding section was cemented to an electromechanical driving unit after final assembly of the various parts.

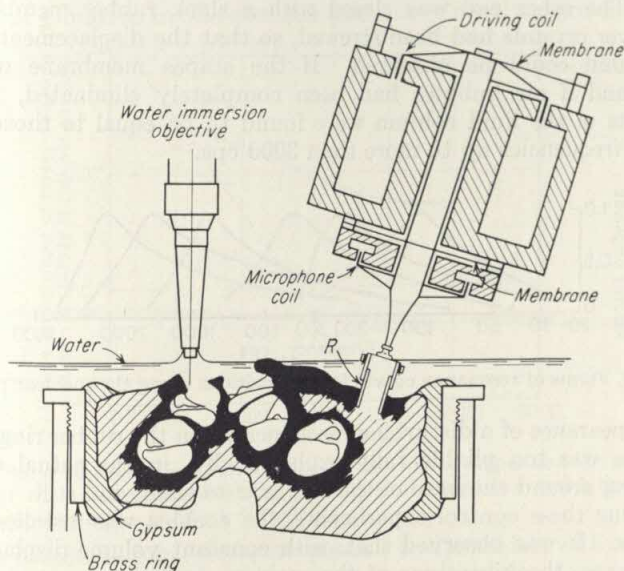


FIG. 11-48. Method of measuring the amplitude of vibration of the cochlear partition in response to volume displacements of the stapes.

Because the presence of even a small air bubble in the cochlear lumen could invalidate the observations, the cochlea was well flushed out with saline solution by way of the tube *R* for several minutes before assembly of the parts. The rubber membrane was installed on tube *R* under water. To avoid the production of bubbles from the considerable amount of air that was in solution in the water, the several parts were heated to 30°C before assembly and cooled to room temperature along with the water before the measurements were made. Because the solubility of air in water increases as the temperature falls, microscopic air bubbles were eliminated.

In order to measure vibrations at the stapes, the electromechanical vibrating system was equipped not only with a driving coil (see Fig. 11-48) but also with a second measuring coil in which an electric potential

was induced. Given an artificial stapes of known base area, this potential made it possible to read off directly the volume displacements of the stapes.

There was another possible source of error besides that of leaving air bubbles in the cochlear lumen. If the rubber ring surrounding the stapes was not stiff enough, the fluid column in the cochlea, in combination with the membrane on the ring, constituted a system capable of vibration that could produce a false resonance.

In order to examine this source of error, a capillary tube full of water was substituted for the cochlea before the measurements. The tube corresponded to the cochlea in length and diameter. One end was closed by the rubber membrane in question, together with the artificial stapes. The other end was closed with a slack rubber membrane on which silver crystals had been strewed, so that the displacements of the fluid column could be observed. If the stapes membrane was stiff enough, and if air bubbles had been completely eliminated, the displacements of the fluid column were found to be equal to those of the stapes at frequencies up to more than 3000 cps.

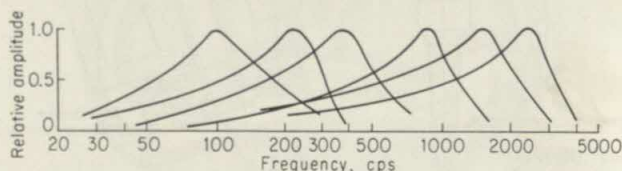


FIG. 11-49. Forms of resonance curves for six positions along the cochlear partition.

The appearance of a disturbing resonance when the rubber ring around the stapes was too pliable fully explains why, in the actual ear, the fibrous ring around the base of the stapes is so small and stiff.

Following these control experiments, the cochlea was installed in the apparatus. It was observed that, with constant volume displacements at the stapes, the vibrations of the cochlear partition were unchanged when the tube *R* was lengthened. It could also be seen clearly that the small silver crystals scattered over the partition clung fast to it and vibrated exactly in phase with it.

Stroboscopic illumination was used throughout the observations, because it permitted the measurement of vibrations that were significantly smaller than could be measured under ordinary illumination.

The curve of transmission of vibration was plotted as follows. A point on the cochlear partition was selected under the microscope, and, with constant amplitude at the stapes, the amplitude at this point was measured as a function of frequency. The resonance curves given in Fig. 11-49 were obtained for various points on the partition; their maximum amplitudes were taken as unity. The data exhibited relatively little variability, and agreement among different specimens was strikingly close. The curves were relatively flat, and in the range between 200 and 3000 cps could be brought into tolerably good coincidence by

parallel displacement along the abscissa. Below 200 cps there appeared a further flattening of the curves, and this flattening increased steadily as the frequency fell further. It is clear that this sort of mechanical analysis of frequency is inconsistent with the requirements of many theories of hearing.

Auditory Threshold as a Function of Hearing. As previous measurements have demonstrated, the transmission of sound pressure from the external meatus to the stapes is independent of frequency up to approximately 2000 cps. Therefore the strong dependence of the auditory threshold on frequency, represented in Fig. 11-50 by the broken line, must arise in the cochlea rather than in the middle ear. It was often assumed in earlier reflections on auditory theory that the maximum amplitude of vibration in the cochlear partition directly represented the

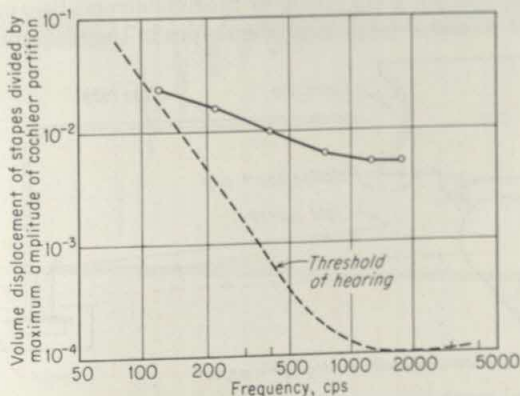


FIG. 11-50. Ratio between the volume displacements of the stapes and the maximum amplitude of the cochlear partition as a function of frequency (solid line). The broken line represents the auditory threshold.

magnitude of stimulation. It is now possible to determine, with constant amplitude at the stapes, how the maximum amplitude of vibration in the partition varies with frequency. For this purpose it is only necessary to determine, from the resonance curves on which Fig. 11-49 is based, the volume displacement per millimeter of length of the partition for maximum amplitude, and to divide this value into the corresponding volume displacement of the stapes.

The displacement of Reissner's membrane, which was the part of the cochlear partition generally observed, changed in form only slightly with frequency. Therefore, the amplitude as expressed in centimeters could be substituted directly for the volume displacement per millimeter of length of the cochlear partition. Figure 11-50 shows how the peak amplitudes varied with the frequency. Unlike this relatively flat function for displacement, the auditory threshold falls by approximately the fourth power of the frequency change as frequency increases. It follows that the magnitude of stimulation in the cochlea cannot be inferred directly from the maximum amplitude of displacement in the partition.

At the same time, it should be pointed out that the rise in the auditory threshold above 2000 cps should not be attributed solely to decreased transmission of vibration from the eardrum to the stapes. It also happens, especially in pathological ears, that the volume displacements transmitted to the cochlear fluid may diminish if the walls of the other parts of the labyrinth near the stapes are not stiff enough.

Travel Time for Pulses along the Cochlear Partition. Not only the resonance curve of the cochlea but also the growth and decay periods of the vibrations are of interest. Essentially the cochlea is a tube with flexible walls. A shock wave therefore takes a certain length of time to travel from stapes to helicotrema. The existence of this travel time has already been demonstrated by a subjective method (page 318). In this method one ear was continuously stimulated by a low tone and the other by a high tone until the area near the helicotrema became insensitive in the first ear, as did the area near the stapes in the second ear. If both

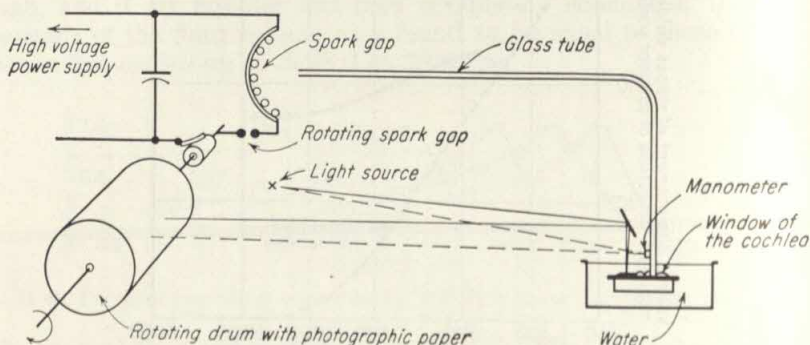


Fig. 11-51. Equipment for measuring the travel time of pulses along the cochlear partition.

ears were then simultaneously stimulated by a sharp click, there was a certain time difference between the perceptions of the two ears as a result of the travel time. This time difference could be demonstrated by a shift in the lateral direction of the perceived position of the click.

In order to measure the travel time objectively, a small mirror (0.05 mm thick, 0.5 mm long and wide) was placed on the cochlear partition, and the stapes was activated by a click. The time difference between the first movement of the stapes and the similar first deflection of a given point along the partition was registered on an oscillograph. An electric spark furnished the click, as shown in the arrangement diagrammed in Fig. 11-51. A rotary spark gap was coupled to the oscillograph drum so that the timing of the spark could be set exactly. A glass tube approximately 1.5 meters long conducted the report of the spark to the cochlea, where a small manometer was inserted to register the arrival of the wave.

It is known that the sound of a spark consists in a sudden rise in pressure followed by a longer period of reduced pressure, such that the integral of pressure change over the total time interval is zero. Because of the long-lasting negative pressure, the onset of any resonant vibration

produced by the click will be somewhat distorted, unless the period of the click is less than one-quarter of the natural period of the vibrating system. Since the duration of a click depends on its energy, it seemed wise to measure this effect in a number of cases. For this purpose, the click was transmitted to a taut rubber membrane equipped with a small mirror. If the total duration of the click was short enough, entirely regular curves of decay were obtained, with a constant ratio between the

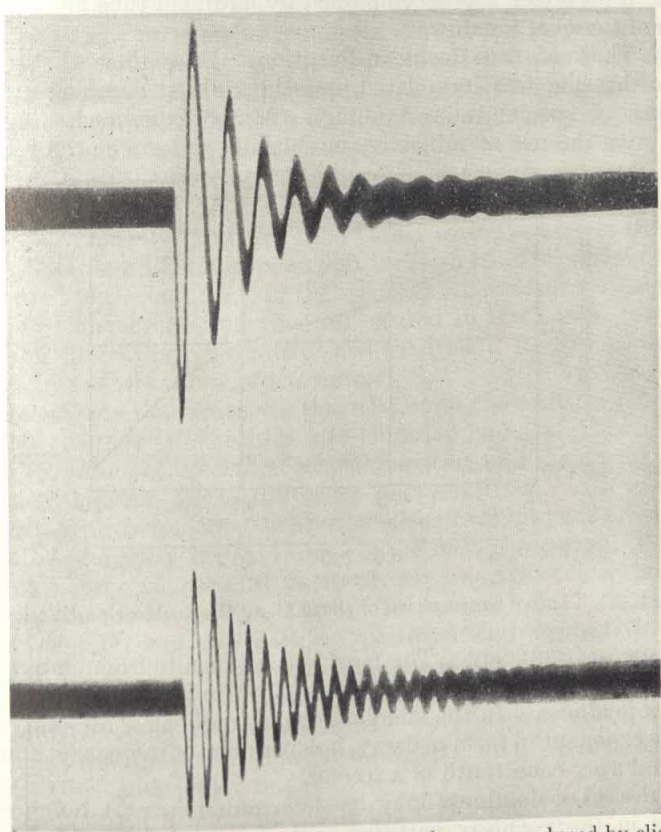


FIG. 11-52. Oscillograms of vibrations in membranes, produced by clicks.

amplitudes of successive waves as illustrated by the upper oscillogram in Fig. 11-52. On the other hand, if the click was long in comparison with the natural period of vibration of the membrane, then the amplitude of the first deflection was diminished by the negative pressure, as shown in the lower oscillogram. It could be determined in this way to what natural frequencies a particular spark was suited. In order to shorten the duration of the click, the free play of the spark over the electrodes was eliminated by mounting a series of small metal balls at regular intervals on a rod of insulating material (trolitul) bent into an arc.

Travel times were recorded for the cochlear model and for specimens

of the cochlea by means of the apparatus shown in Fig. 11-51. The values given in Fig. 11-53 are representative of all the measurements. The abscissa gives the distance from the stapes, while the scale below indicates the frequency corresponding to each point.

Control experiments demonstrated that travel time was unaffected by changes in the stiffness of the membrane of the cochlear window receiving the pulse, or by increasing the length of the vibrating fluid column. This latter was accomplished by adding a tube filled with fluid in front of the oval window.

Decay Time of the Cochlear Partition. Ever since the resonance theory of hearing was formulated, questions about damping and decay have been of special interest (Jung). Many experiments have been devised with the use of subjective methods to determine the relation of

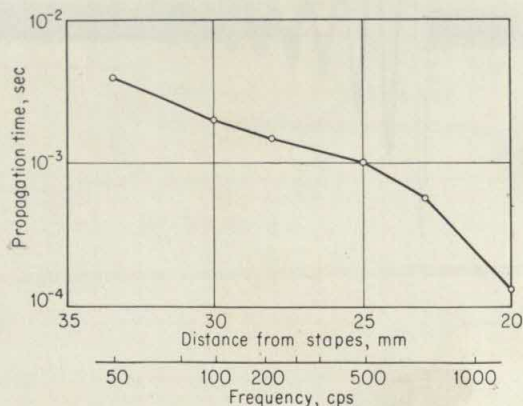


FIG. 11-53. Time of propagation of clicks along the cochlear partition.

decay time to frequency. The most precise results from an experiment of this type were obtained by Steudel (2), who investigated the rate of decline of loudness. In the middle range of frequencies his study showed a strictly exponential form of decay, independent of frequency, amounting to 18 db during each tenth of a second.

This decay of loudness may be determined in part by mechanical damping in the cochlear partition and in part by the rate at which neurochemical processes fall off, a rate which generally, as in other fields of physiology, declines exponentially. In order to determine which of these two factors is more significant, the decay of vibratory sensation on the skin was investigated. In the skin there are no resonant mechanical elements, and the cause of decay must be entirely neural. The decay time measured was so large that we can properly assume that both on the skin and in the ear it is the neural decay time that is predominant. Consequently, the earlier subjective techniques are not useful in measurements of the mechanical damping of the cochlear partition.

If a resonance curve is fitted empirically to the data represented by the curves in Fig. 11-49, we obtain a value for the logarithmic decrement,

$\delta = \pi(\Delta f/f_r) = 1.3$, in which Δf is the difference between the frequencies of the two half-power points, and f_r is the resonant frequency. This measure of damping turns out to be independent of frequency above 200 cps and increases somewhat below this point.

In order to measure the decay period of the cochlear partition directly, the model of the ear was subjected to a sound pulse from a spark, making use of the arrangement shown in Fig. 11-51. The vibration of the rubber membrane of the model with its attached mirror was recorded by an oscillograph. The progressive change in the natural period of vibration could easily be followed as the distance from the stapes was increased. It was also apparent that the natural frequency at a given point on the membrane always coincided with the frequency that produced the maximum amplitude of sinusoidal vibration.

Unfortunately, the corresponding experiment with specimens of the ear was unsuccessful. The measurements of the decay process could not be reproduced exactly, and the time varied with the size of the mirror used, an effect that did not appear with the model. This difference could be attributed to the fact that, in the specimen, the mirror was laid on top of Reissner's membrane and was not secured to the basilar membrane. The soft tissue between the mirror and the basilar membrane produced distortion in the vibrations of the mirror.

The easiest way to investigate this relation of the mirror to the basilar membrane was to set the cochlea into vibration and observe stroboscopically the vibrations of both the cochlear partition and the mirror. There was usually a clear phase difference between them, and this difference varied with frequency. Only the silver crystals, which were very small, followed exactly the vibrations of the basilar membrane.

A direct measurement of the decay process was again attempted using the apparatus shown in Fig. 11-48. Very small silver crystals were scattered densely over the cochlear partition and exposed to strong, constant illumination. When the partition was set into vibration, the vibrations could be seen to die away as the microscope was moved slowly at right angles to the axis of vibration. Very regular curves could be obtained in this way if the silver crystals were small enough and if the illumination was sufficiently bright.

A rotating mirror in an eyepiece is the best equipment for spreading out the vibrations for observation. An alternative is illustrated in Fig. 11-54, in which the microscope pedestal was made fast in a rubber mounting. This arrangement permitted the microscope some freedom of lateral movement without affecting its normal focus. An eccentric weight which could be rotated by a flexible shaft was then fastened to the housing of the microscope. When the weight was rotated at the rate of 10 rps, the microscope described small circular movements. The flexible shaft was connected to a rotary switch, which always cut off the current to the electromechanical driving system (see Fig. 11-48) when the circling microscope was at a certain position. Thus the microscope gave a picture of the course of the decaying sinusoidal vibration, as shown in Fig. 11-55.

This technique was then applied to the measurement of the decay process of the cochlear partition when the ear was subjected to brief pulses produced by either direct current or a sinusoidal current switched on and off. For the whole frequency range and for all positions on the

cochlear partition measurements were obtained in which the ratio of the amplitudes of two successive deflections in the same direction lay between 4:1 and 6:1. This corresponds to a logarithmic decrement,

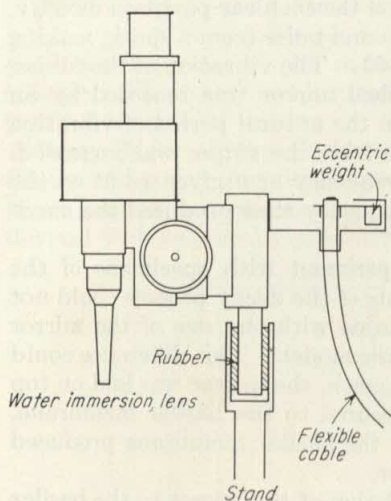


FIG. 11-54. Method of measuring the decay time of the amplitudes of movements of the basilar membrane.

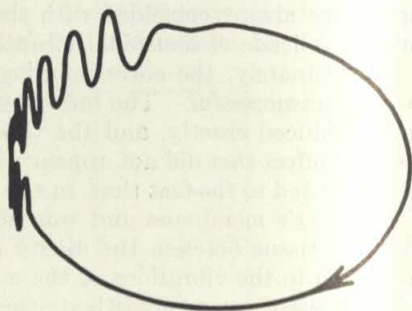


FIG. 11-55. Form of oscillogram obtained with the equipment shown in the preceding figure.

$\vartheta = \log_e A_1/A_2 = 1.4$ to 1.8 , in which A_1 and A_2 represent the amplitudes of successive excursions. This measure of ϑ should be numerically equivalent to the value of ϑ derived from a resonance curve.

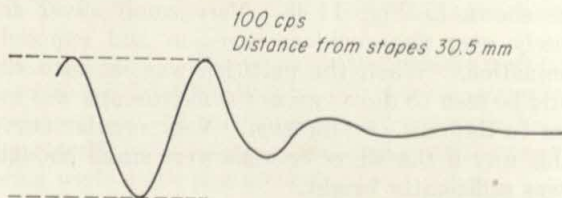


FIG. 11-56. The decay of amplitude in a portion of the cochlear partition 30.5 mm from the stapes, driven at its natural frequency of 100 cps.

Figure 11-56 reproduces the decay process when a point on the partition 30.5 mm from the stapes was driven at its resonant frequency of 100 cps.

VARIATIONS OF PHASE ALONG THE BASILAR MEMBRANE*

The phase relations in the movements of the cochlear partition possess a significant theoretical interest. If for some particular point along this partition the changes of amplitude are plotted as a function of frequency, a curve is obtained that strongly resembles a resonance curve. Such

* Article 47 as listed in the Author's Bibliography. Published in 1947.

observations seem to support the notion of an aural resonator. In a simple resonant system, however, the phase angle must change from $\pi/2$ through zero to $-\pi/2$ as the driving frequency is changed continuously. Furthermore, at the point of resonance the phase angle will be zero. The measurement of phase is therefore particularly suited to test the correctness of this simple view.

The phase relationships in the movement of the cochlear partition were observed by means of the phase-measuring stroboscope described in Chap. 4, page 38. It was first determined that there are no phase differences among the movements of the basilar membrane, the organ of Corti, and the tectorial membrane. In a fresh preparation, Reissner's membrane also vibrates in phase with the other parts of the partition. At the higher frequencies it was sometimes observed that Reissner's membrane did not undergo a simple movement, but vibrated in sections.

In Fig. 11-57 is shown the form of vibration of a point along the cochlear partition 33 mm from the stapes. The vibratory amplitude is shown by

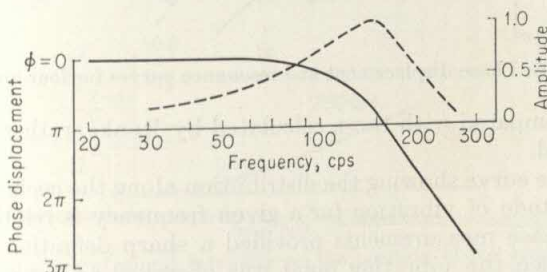


FIG. 11-57. Phase displacement (solid line) and resonance curve (broken line) for a point on the cochlear partition 30 mm from the stapes. The phase angle is relative to the stapedial motion.

the dashed line as a function of frequency when the stapes was driven with constant amplitude. The form of the curve is similar to a resonance curve. The solid line in this figure gives measurements of the difference in phase angle between the stapes and the point of measurement for the various frequencies. As the resonance curve is traversed, the phase angle changes from $\phi = 0$ to $\phi = 3\pi$. These facts, taken together, clearly indicate that we are not dealing with a simple resonance but with traveling waves, whose wavelength becomes shorter as the frequency increases, and which pass by the point of measurement.

The distribution of amplitude and phase angle along the cochlear partition is shown in Fig. 11-58 for four frequencies. Below 50 cps the movement of the entire cochlear partition is practically in phase, whereas above 150 cps a traveling wave can be demonstrated. The measurements were carried out without difficulty and were fully reproducible in a given cochlea. In different cochleas there were displacements of the resonant peak along the partition, displacements that were always associated with equally great displacements of the phase angle.

In Fig. 11-58 the movement of the cochlear partition is presented in terms of its magnitude and phase. By using the curve for 200 cps, the

detailed form of vibration of the partition was calculated for two different instants in time separated by a phase angle of 90° . The two curves obtained in this way are shown in Fig. 11-59. The abscissa represents the distance from the stapes, while the thin-dashed enclosing curves represent the maximum amplitude at each point. If the measured

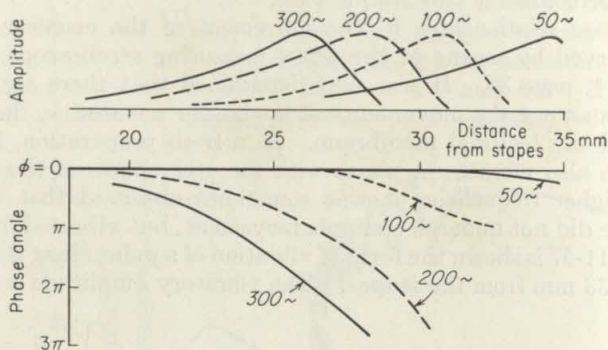


FIG. 11-58. Phase displacement and resonance curves for four low tones.

values are compared with those calculated by Ranke, rather good agreement is found.

Though the curve showing the distribution along the cochlear partition of the amplitude of vibration for a given frequency is relatively flat in form, the phase measurements provided a sharp definition of position, especially when the vibrating point was observed as it passed through the resting position. Phase measurements therefore are particularly suitable for the exact determination of small displacements of the pattern

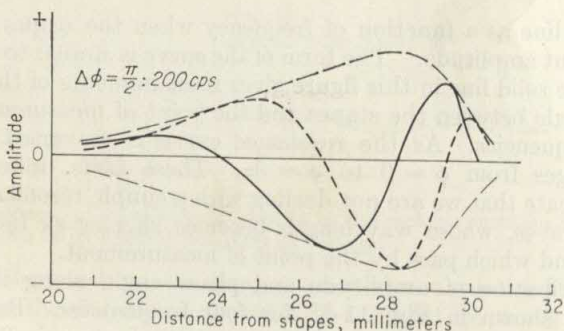


FIG. 11-59. Detail of the form of vibration of the cochlear partition for 200 cps at two instants within a cycle.

of vibration, especially as these usually cannot be determined from the pattern of amplitude. For the same reason, however, the phase measurements were especially disturbed if too great an opening of the cochlear canal was made in order to carry out the measurements. Hence, it was possible here to work only with extremely small observation windows.

The larger the number of waves lying between the stapes and the point of measurement, the greater was this error in the measurement of phase.

Nonlinearity in the Vibration of the Cochlear Partition. It has long been known in musical circles that a pure tone of less than 800 cps becomes lower in its apparent pitch when the loudness is increased. Measurements of this phenomenon have recently been carried out by Zurmühl and by Stevens. It may be asked whether this change of pitch is produced mechanically by a change in vibration of the cochlear partition or whether it should be attributed to nervous processes. To answer this question the phase difference between the stapes and a point on the partition 30 mm from the stapes was measured as the amplitude of vibration was varied. For a pure sine wave of 200 cps the relationship shown in Fig. 11-60 was obtained, in which the amplitude of vibration of the partition is given as the abscissa and the ordinate shows the change in phase difference between the stapes and the point of measurement as the amplitude is increased. It appears that with increasing amplitude

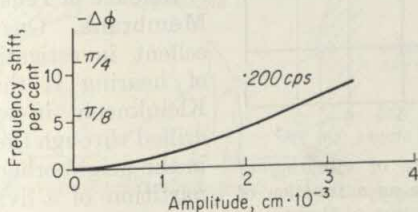


FIG. 11-60. The effect of sound intensity on the position of the response along the cochlear partition. The ordinate shows the percentage of change in frequency necessary to keep the response pattern in one place as the sound amplitude was changed. The frequency shift is also expressed as a phase change.

the phase difference between the stapes and the point of measurement steadily decreases; that is, the wavelength becomes larger and the pattern of vibration is displaced toward the helicotrema. This corresponds to a lowering of the pitch of the tone. In order to obtain a measure of this shift in the pattern, the phase change produced by the increase in amplitude was compensated by raising the frequency until the original phase angle between the stapes and the point of measurement had been restored. The necessary percentage change in frequency is also shown in Fig. 11-60.

These measurements show that with increasing amplitude of vibration the cochlear partition becomes less elastic. This increase in the stiffness of the membrane may be demonstrated directly by relating the amplitude of vibration of the cochlear partition to the amplitude at the stapes as the latter is increased. In order to carry out these measurements properly, the effective area of the artificial stapes was chosen so that its excursion was approximately as large as the movement of the cochlear partition. Corresponding pairs of values, obtained with a tone of 200 cps and a point of measurement 30 mm from the stapes, gave the curve shown in Fig. 11-61. As the amplitude is increased, the movement of the basilar membrane is clearly not proportional to the movement of the stapes.

The measured mechanical changes in the cochlear partition lie in a direction that would explain the expected lowering of pitch with an increase of loudness. Nevertheless, this appears only with an amplitude of vibration above the threshold of feeling in normal hearing. As earlier measurements have shown (page 258), the threshold of feeling for 200 cps is about 2×10^3 dynes per sq cm (140-db sound-pressure level). The volume displacement of the stapes corresponding to this sound pressure has been shown (page 432) to be 1.4×10^{-6} cu cm. The amplitude of vibration of the cochlear partition that corresponds to this volume displacement at 200 cps was calculated in an earlier series of measurements

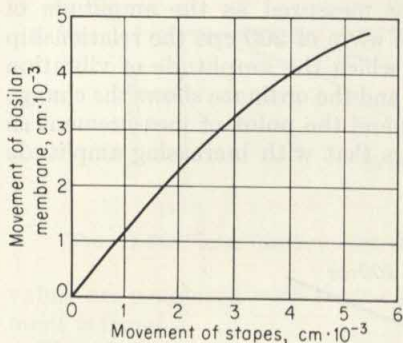


FIG. 11-61. Amplitude of vibration of the basilar membrane as a function of the amplitude of vibration of the stapes, measured at a point 30 mm from the stapes with a tone of 200 cps.

(page 455) as 7×10^{-5} cm. These measurements indicate that most of the known changes of pitch with changes in loudness have their origin in neural rather than mechanical processes.

Release of Tension in the Basilar Membrane. One of the more excellent investigations in the field of hearing is that of Held and Kleinknecht in which a hole was drilled through the cochlear capsule in the neighborhood of the cochlear partition of a living guinea pig in such a way that the tension on the fibers of the cochlear partition was changed over a small region. This

mechanical disturbance in a narrow and limited region produced a disturbance of auditory sensitivity in the form of a tonal gap. It is uncertain whether this injury actually altered the vibratory characteristics of the cochlear partition in a mechanical way or whether the tonal gap was produced by secondary nervous effects of the injury.

With this method of investigation the mechanical change may be produced, as pointed out by Kleinknecht, either because the membrane is under increased tension or because it is loosened. An increase in tension might arise because the internal pressure forced the spiral ligament and basilar membrane out through the hole in the bony wall. Yet this internal pressure and its effect cannot be large. In one of the histological illustrations a layer of fibers covering the drilled opening shows no bending at all, suggesting that the fibers were not pressed into the drilled opening. Consider further that, for the production of a demonstrable tonal gap, at least a hundredfold change in the auditory threshold is required, and this threshold change would require that the tension of the basilar membrane be increased by the same factor. With the relatively great pliability of the membrane, such pressure would necessarily result in visible histological displacement. It seems highly improbable that the tension of the basilar membrane could be raised to a point at which the form of vibration would be changed.

The appearance of a tonal gap when the basilar membrane is loosened rests on the assumption that the basilar membrane consists of fibers that are under tension and whose sensitivity is significantly increased by resonance. If the natural frequency of these fibers is changed, any increase in sensitivity caused by resonance will be lost. The relative flatness of the measured resonance curves indicates that theoretically we cannot expect a marked decrease of the amplitude of vibration with the release of tension at the affected point. On the contrary, anatomical investigations have shown that at the beginning of a tear in the basilar membrane the amplitude of vibration becomes larger, rather than smaller, because the membrane becomes more pliable.

Though an increase in the tension of the basilar membrane can be produced only with difficulty it is easy to decrease the tension. For

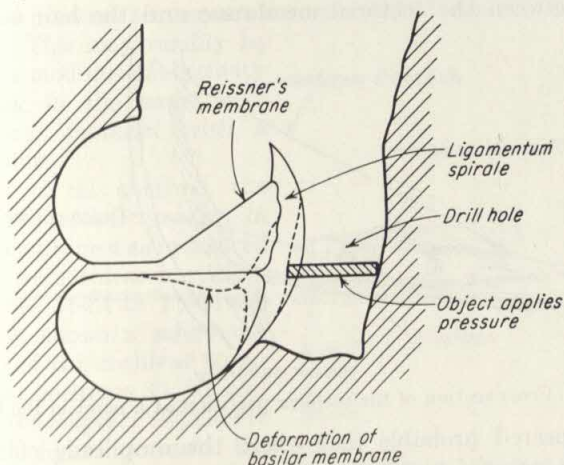


FIG. 11-62. Method of relaxing the tension of the basilar membrane.

this purpose the experiment of Held and Kleinknecht was repeated. After drilling through the cochlear capsule of the guinea pig no change in the form of vibration could be observed. In the human ear this experiment could be carried to the point, as shown in Fig. 11-62, where the bone in the neighborhood of the spiral ligament was bored out for a distance of about 0.6 mm; and then, by means of a probe, the basilar membrane was not only released from tension but was actually compressed so that it was bent out sharply to the side.

Careful measurements showed that this bending of the basilar membrane had not the slightest effect either on the distribution of the amplitude of vibration or on the distribution of phase as measured with the phase stroboscope. This experimental result agrees with the earlier observation that the basilar membrane is not under tension but forms an unstressed, gelatinous, elastic plate. Since tonal gaps are not produced by a mechanical change in the form of vibration of the cochlear partition, they must be the result of a disturbance of the nerve fibers or the end organs.

Mechanical Structure within the Cochlear Partition. After the mode of vibration of the cochlear partition had been investigated as a whole, the question remained whether all the different membranes making up the partition carry out the same movement, or whether they show differences because of their varied stiffness. Figure 11-63 shows a schematic section through the beginning of the first turn of the human cochlea (Held). The triangular cochlear duct is closed above by Reissner's membrane and is bounded below by the spiral ligament, the basilar membrane, and the bony portion of the cochlear partition. The entire cochlear duct is filled with a thin fluid mass. Of special interest are the outer and inner hair cells which are carried on the arches of Corti and on which the nerve fibers end. The tips of the hair cells are covered by the tectorial membrane. In many illustrations no direct connection is shown between the tectorial membrane and the hair cells. In the

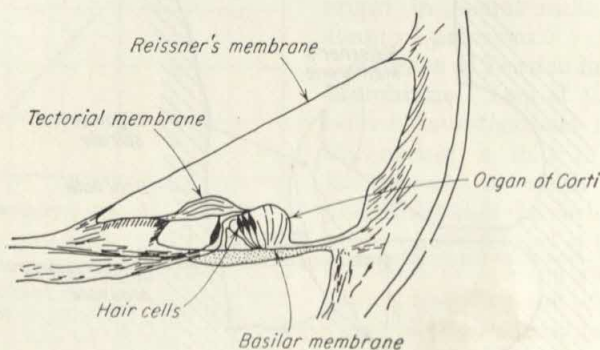


FIG. 11-63. Cross section of the cochlear partition at a point in the basal turn.

past, it appeared probable that where the amplitude of vibration is greatest the tectorial membrane might come into contact with the hair cells and produce in this way the stimulus for hearing. More recent histological preparations when carried out carefully have shown that the tectorial membrane is attached to the hair cells. This attachment was frequently observed in fresh preparations. It was always found on dissecting the material that the tectorial membrane adhered to the hair cells as it was drawn away and was free of the remainder of the organ of Corti only in the region behind the hair cells.

If Reissner's membrane was removed along the cochlear partition it was easily seen with the phase stroboscope that the tectorial membrane, the organ of Corti, and the visible part of the basilar membrane vibrated completely in phase, so that it is proper to consider the entire cochlear partition as a single structure. It must still be decided which of the three membranes determines the volume elasticity of the partition. There has been much discussion in the medical literature of the relative importance, in this connection, of the tectorial membrane and the basilar membrane.

Because of the extraordinarily small size, softness, and largely inaccessible location of the various tissues it appeared to be most practical

to investigate their elastic properties by means of the fine hairs used to measure sensitivity to touch.

For this purpose a piece of hair 3 to 10 mm long and as straight as possible was fastened at one end to a small stick. If the end of such a hair is pressed perpendicularly against a surface, the pressure on the surface increases until the resistance to bending of the piece of hair is overcome. Pressing further does not result in any further increase in the pressure exerted. In this way a known maximum pressure can be produced which can be changed by altering the length and diameter of the hair. This maximum pressure is easily measured with a balance, preferably a spring balance. With the effective pressure on the surface determined in this way, the depth of the depression made by a given hair was determined microscopically. The depth of the depression divided by the pressure serves as a measure of the elasticity of the surface in question. This may readily be reduced to the modulus of elasticity by measuring in the same way a homogeneous material with a known modulus.

By the use of this method, the depth of impression made in Reissner's membrane was measured along the entire cochlear partition. In each of Figs. 11-64 to 11-66 the upper portion shows a schematic cross section of the cochlear partition of man at positions 30, 20, and 10 mm from the stapes. The lower part of each figure presents the depth of impression, expressed in centimeters per dyne, for the positions across the membranes corresponding to the section shown immediately above. In each figure the measurements of Reissner's membrane are represented by the thin continuous line *R*. A comparison of the three figures shows that Reissner's membrane has the

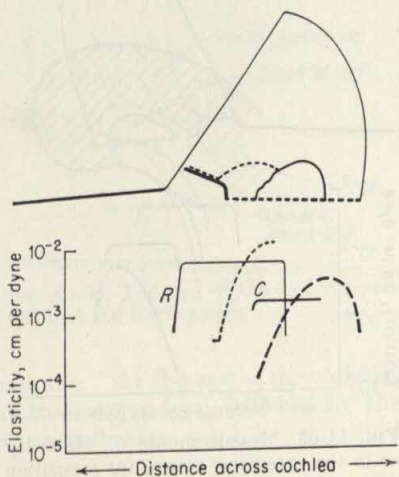


FIG. 11-64. Elastic properties of cochlear structures at a point 30 mm from the stapes. *C*, organ of Corti; dotted line, tectorial membrane; *R*, Reissner's membrane; dashed line, basilar membrane. Above the graph is a schematic outline of the structures.

same elasticity throughout its entire length.

If Reissner's membrane was removed and the material within the cochlear duct was washed away, the elastic properties of the tectorial membrane could be investigated in the same manner. These measurements had to be carried out under water to avoid the effects of drying and the effects of capillary forces. The values obtained for the tectorial membrane are shown in the figure by the dotted lines. The stiffness of this membrane is not great and increases slightly only in the neighborhood of the stapes. This membrane is noteworthy for the ease with

which it may be moved in a direction perpendicular to the basilar membrane. Together with its supporting structure it represents essentially a flat, delicate, thin-walled tube filled with fluid and which can be rotated about the side that consists of the bony shelf of the cochlear partition. The decrease in elasticity at the end near the stapes is a result principally of its narrow breadth, which reduces the lever arm and supports the entire membrane more firmly from below.

The values for the organ of Corti (including the hair cells), shown in the figures by the heavier continuous line *C*, indicate no dependence whatsoever on their location. On the other hand, it can be seen from the heavy

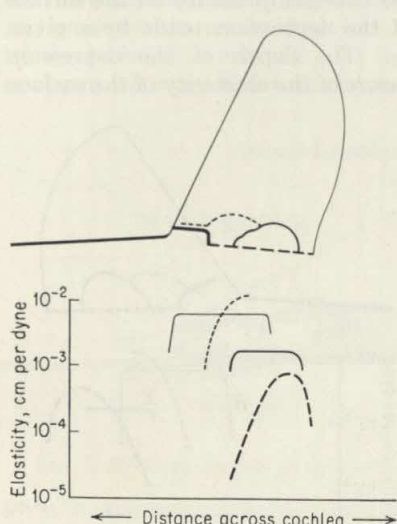


FIG. 11-65. Measurements on elasticity as in the preceding figure, for a position 20 mm from the stapes.

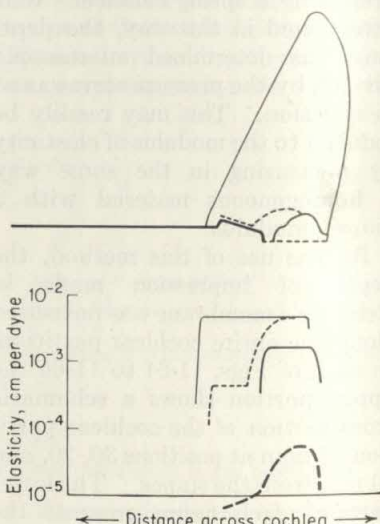


FIG. 11-66. Measurements on elasticity as in Fig. 11-64, for a position 10 mm from the stapes.

dashed lines in the figures that there are marked differences in the stiffness of the basilar membrane from one position to another. These changes in the basilar membrane produce a continuous change in the volume elasticity along the cochlear partition. The measurements show that it is not the tectorial membrane (Hardesty) but, as Hensen (1) and Helmholtz (1) have argued, the basilar membrane that determines the movement of the cochlear partition and the location of the point of maximum vibration.

When the shape of the depression in the surface produced by the test hair was examined, all of the surfaces investigated showed a circular depression except the tectorial membrane. This membrane, as seen in Fig. 11-67, presents a much-elongated hollow. It exhibits a different elasticity in the transverse direction than it does lengthwise. In the latter direction it possesses a substantial stiffness. This condition may be recognized also from the fact that upon tearing it away from its

attachment a considerable length comes off, whereas the other membranes may be removed in small sections. It may be assumed that this longitudinal stiffness of the tectorial membrane produces a pressure drop along the cochlear canal, the distribution of which favors a frequency analysis.

From the measurements of Figs. 11-64 to 11-66 it is seen that the two other layers of cells with constant structure are superimposed upon the basilar membrane with its changing elasticity. This view is supported by an inspection of the end of the cochlear partition at the helicotrema, as shown schematically in Fig. 11-68. Set out on the flat basilar membrane that stretches between the bony walls, the tectorial membrane and the organ of Corti are like two parallel pads which at their ends clearly

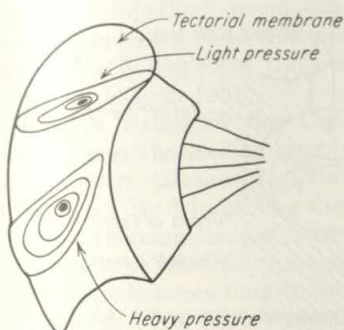


FIG. 11-67. Depressions of the tectorial membrane produced by test hairs, seen from above.

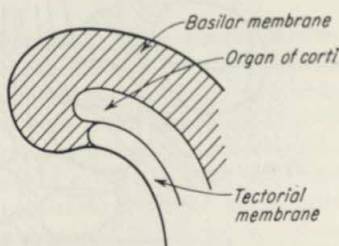


FIG. 11-68. The end of the cochlear partition at the helicotrema.

stop short of the end of the basilar membrane. At the end of the cochlear partition it is the tectorial membrane that stops first, followed by the organ of Corti and finally by the basilar membrane.

ELASTICITY OF THE COCHLEAR PARTITION*

As can be seen in Fig. 11-69, the cochlea consists of a tube of roughly circular cross section buried in the hard, petrous portion of the temporal bone. This tube is divided throughout its length into the scala tympani and scala vestibuli by a wall, the cochlear partition. The partition is made up of bone on the edge toward the axis of the cochlea. It becomes more elastic toward the outside of the cochlea and thins out finally into the basilar membrane. Seated astride the partition is the organ of Corti, in which the fibers of the auditory nerve terminate after entering by way of the cochlear axis and piercing the bony wall of the cochlear canal. The auditory end organ, the organ of Corti, is actually located in the cochlear duct, which forms in effect a triangular enlargement of the cochlear partition. The cochlear duct is bounded on the one side by the basilar membrane, and on the other side its viscous contents are contained

* Article 39 as listed in the Author's Bibliography. Published in 1941.

by the thin Reissner's membrane. Both the basilar membrane and Reissner's membrane are supported by the fibrous tissue of the spiral ligament on the outer wall of the cochlea.

The canals of the cochlea are filled with fluid. The oscillatory movements of the footplate of the stapes are transmitted to the fluid in the scala vestibuli and then by way of Reissner's membrane to the basilar membrane and its associated nerve endings. The displacement is equalized by way of the scala tympani, which leads back to the middle ear, from which it is closed off by the membrane of the round window. The cochlear partition ends short of the apex of the cochlea, leaving an opening between the two scalae through which any static difference in pressure on the two sides of the partition can be equalized.

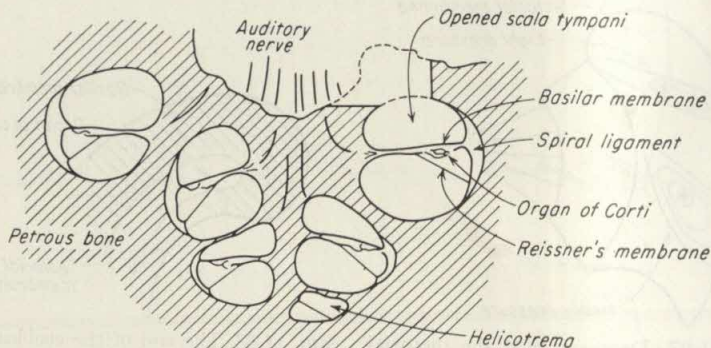


FIG. 11-69. Preparation of a human temporal bone for measuring the tension of cochlear structures.

The cochlea of man and other mammals was discovered in 1561.* The phenomenon of the sympathetic resonance of two strings in tune with each other was first observed in the middle of the seventeenth century in the forerunners of the modern pianoforte, although in ancient times resonance could probably have been observed in harps. Du Verney, in 1683, was the first to propose resonance as the basis of perception of sound. At that time the bony region of the cochlear partition was thought to be the resonator. Because this bony spiral gradually narrows toward the apex of the cochlea, it was assumed that vibrations of high frequency produced sympathetic vibration at the apex.

Because changes of pressure in the cochlear duct would produce vibrations of greater amplitude in the more flexible region of the partition than in the bony region, it seemed logical to locate sound perceptions in the more flexible part. Cotugno first advanced this notion in 1760. And because the more flexible section widens progressively toward the cochlear apex, it followed that the deeper tones should be localized at the apex, a localization that has now been confirmed experimentally. Hensen in 1863 advocated the view that, among the membranous

* For a more detailed account, see Held, and also Schäfer and Giesswein.

structures of the partition, the basilar membrane was the one under greatest tension so that it must be the site of the resonance.

The difficulty of conceiving that sharply localized vibrations, such as those of piano strings, might occur in a membrane led Helmholtz (1) to investigate the conditions under which such vibration is possible. His calculations showed that if in a long, narrow membrane the transverse tension is significantly greater than the longitudinal tension, a uniformly applied pressure will set only a narrowly limited transverse strip into vibration not unlike that of a piano string. According to Ohm's law, the perception of a complex sound depends upon its analysis into single tones and is entirely independent of the phase relations of these components (Helmholtz, 1; Ohm). Such a result could only be explained in terms of sympathetic resonance, and the picture of the basilar membrane as a system under transverse tension seemed assured. Further theoretical work entirely neglected the possibility of longitudinal tension until the work of Ranke in 1931.

Tension Ratios of the Cochlear Partition. The simple notion of resonance in the basilar membrane, which likens it to the resonance of piano strings, assumes that the longitudinal tension of the membrane is negligible. By determining the ratio between longitudinal and transverse tensions, therefore, it is possible to discover whether this simple notion is admissible, or whether the actual course of events is more complicated.

The ratio between longitudinal and transverse tensions may readily be determined. If a rubber membrane is stretched uniformly in all directions and a needle is pressed upon it at right angles to the surface, the resulting deformation is circular. If on the other hand the membrane is under greater tension in one direction than the one perpendicular to this, the deformation is elliptical. Directional symmetry is easily demonstrated in this manner in membranes and other elastic materials.

To carry out this experiment on the basilar membrane, the scala tympani was carefully laid open by drilling, as shown in Fig. 11-69, so that the cochlear partition became visible. Under illumination, the bony section appeared white and was clearly visible. Next to it was an elastic zone (the spiral limbus), which appeared gray and exhibited clearly visible radial fibers. The basilar membrane itself was usually visible only because of the fine bone dust that fell on it during the drilling.

To avoid tearing the basilar membrane by an involuntary movement while the needle was touching it, thin glass threads 0.01 to 0.1 mm thick were prepared. The length of the threads was adjusted so that when the thread was tested by pressing down on a balance, the bending point was reached at either 40 or 200 mg. It is characteristic of such threads that once the thread is bent a further movement of the handle produces no greater pressure on the tip. The free end of the glass thread was melted down judiciously to a minute ball in order to distribute the pressure more uniformly. In preliminary experiments, hairs of the head were a good substitute for glass threads, as their bending point could be adjusted easily by cutting them shorter. They were chosen from 7 to 40 mm in length and were cemented to a handle that was as light as possible.

The observations performed with these hairs showed that near the cochlear apex where the basilar membrane is broad the area of deformation was perfectly circular, as indicated in Fig. 11-70, even when the pressure was not exerted at the center of the membrane. Near the stapes the deformed area was an ellipse with its longer axis running longitudinal to the membrane. The ratio of the two axes was

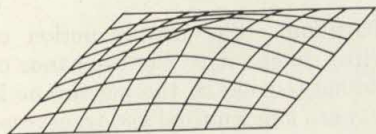
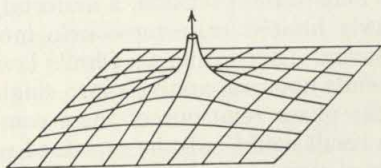


FIG. 11-70. Impressions produced by exerting pressure on a uniformly stretched membrane, upper drawing. The basilar membrane in the region of the apex responds in a manner as shown in the lower drawing.

1:2 at most. Very thin glass threads had to be used here, so that the deformed area would be small compared to the width of the membrane. A microscopic enlargement of about thirty times was used.

It follows that, in any case, the most flexible part of the cochlear partition displays essentially the same elastic properties in the longitudinal and transverse directions. This independence of direction in the elastic properties of the basilar membrane depends in part on the existence, in addition to the radial fibers, of a layer lying upon the basilar membrane (the tympanic lamella) whose fibers extend longitudinally along the membrane. As

Roux has demonstrated, such sets of fibers at right angles to each other are of frequent occurrence in tissues, as, for example, in the eardrum.

If the hair probe was used not on the basilar membrane but on the spiral limbus then a considerable length of this zone, up to one-eighth of a turn, was always displaced simultaneously. At the same time, the basilar membrane was displaced over the same distance. The spiral limbus therefore possesses considerable rigidity in the longitudinal direction. Figure 11-70 shows in the upper sketch the deformation produced when a rod is pushed into a stretched membrane under uniform tension. The displacement of the membrane increases sharply near the point of application of the pressure. Nothing of the kind was observed in the basilar membrane, where the deformed area was much the same as that produced when a pencil point is pressed into the skin.

The basilar membrane therefore does not seem to act as a membrane under tension. A large part of its elasticity when deformed arises in some other way. The question is whether the basilar membrane at rest exhibits any tension at all.

In the first place, the view that the transverse fibers of the basilar membrane are especially well developed cannot be substantiated. For if the membrane is dissected under the microscope, it turns out to be loose as compared, for example, with the fibers of the auditory nerve. In the second place, any great tension on the basilar membrane is improb-

able for the following reason. It was repeatedly observed during the preparation of specimens that, as the bony wall of the cochlear duct was ground away, there first appeared a thin lining membrane that was firmly attached to the spiral ligament. This membrane and the spiral ligament could easily be loosened from the wall of the bone, so that finally a large section of the cochlear canal, perfectly transparent, stood up supported only by the lining membrane. Third, when a slit is cut in any elastic material or tissue which is under tension, the cut edges gape apart in a lens-shaped opening. But when fine cuts were made in the basilar membrane, transversely or longitudinally, the cut surfaces could not be observed to draw apart.

These observations indicate that the basilar membrane is not under tension and that it can best be likened to a gelatinous sheet covered by a thin, homogeneous layer of fibers. The complete lack of tension in the cochlea would appear to be important physiologically, inasmuch as the internal structure of the cochlea may, as a consequence, be treated as analogous to the other parts of the labyrinth where the tissues have always been regarded as free from tension when there was no effective external stimulation.

It is pertinent to recall in this context those phenomena which indicate what role is played in hearing by steady or gradually changing pressure in addition to the usual alternating pressure of sounds (page 420). If it were true that the membrane was already under strong tension, the slightest change in tension would immediately produce a marked disturbance. In the tension-free cochlea, on the other hand, steady tensions and lasting deformations are, in fact, produced only by sound stimulation. Had early thinking about the physiology of hearing not started with the notion of a vibrating piano string, the basilar membrane might never have been regarded as under lasting tension.

The essential physical characteristic for the displacement of fluid in the cochlea is that, under a given pressure change in one half of the cochlea, a certain volume of liquid per millimeter of length of the basilar membrane is forced into the other half, and this volume depends principally on the rigidity of the intervening partition. The necessary rigidity can be achieved not only by the tension of the elastic layer but equally well by an increase in thickness. Furthermore, the amplitude of deformation A of an elastic sheet can also be altered sharply by a change in its width b , for if p is the liquid pressure exerted uniformly on the sheet, h the thickness of the oblong sheet, and E the coefficient of elasticity, then, according to Hütte, $A = 0.028pb^4/Eh^3$. Thus the variations in width alone of the basilar membrane from cochlear apex to stapes would be enough to achieve the variation in rigidity of the membrane necessary for a frequency analysis.

Static Elasticity of the Cochlear Partition. After it had been shown that the elastic properties of the basilar membrane are closely similar in the longitudinal and transverse directions, the next step was to determine numerically what the elasticity is. Although many theoretical discussions have assumed an increase in flexibility as the apex is approached,

it has not been determined, so far as the author is aware, that the elasticity is a function of locus. The flexibility at one position was measured by Berendes. He investigated how far a rod would sink into the center of the basilar membrane as a function of pressure applied to it. These measurements involved some difficulty in that the basilar membrane is not taut, but rather is a mass with gelatinous layers of various kinds. When a rod is pushed into the membrane, therefore, it first sinks into the gelatinous mass, and only under further pressure does it cause deflection

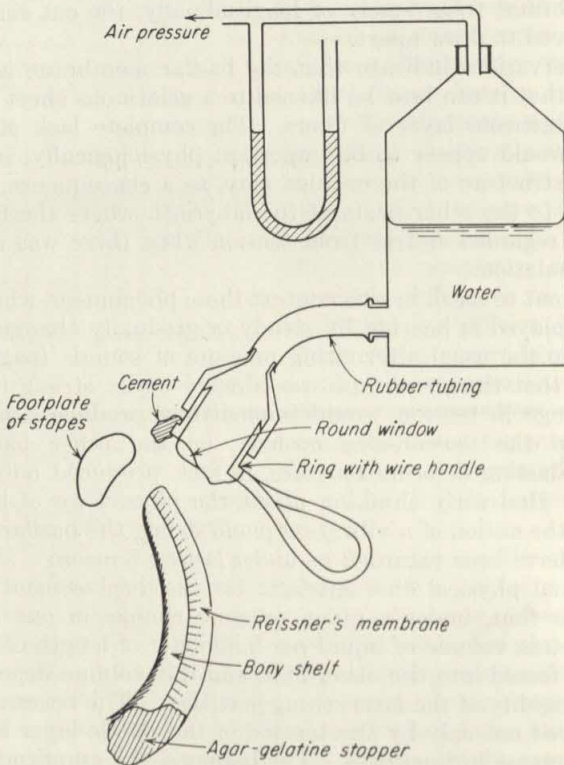


FIG. 11-71. Method of measuring the static elasticity of the cochlear partition.

of the membrane as a whole. Thus any proportionality between pressure and depth of sinking is lost.

Because of the gelatinous surface of parts of the partition, it seemed appropriate to explore the displacement of the partition under the same conditions as obtain in reality, that is to say, under pressure distributed uniformly over the membrane. To this end, the middle ear was sawed in two in a direction perpendicular to the cochlear axis (whose direction was inferred from the course of the auditory nerve), so that both cochlear windows were exposed. The layers of membrane surrounding the round window were carefully removed, and the membrane of the round window

itself was pierced with a pointed drill. As indicated in Fig. 11-71, a small brass ring equipped with a wire loop was set over the round window. The loop could be bent so that the ring fitted nicely on the rim of the window. The ring was hermetically sealed to the rim by zinc oxyphosphate cement. The bone was then submerged in water, and the cochlear apex was opened. It was easy to do this when working from the middle ear, for the position of the helicotrema in relation to the exterior of the bone could be determined from the position of the stapes. Furthermore, as the bony wall is thin here, the inner spiral became visible after a little drilling with a fine burr. It is not difficult to avoid injuring Reissner's membrane when opening the cochlea at this place. After the opening had been made the helicotrema was closed with a warm mixture of agar and gelatin,* so that a pressure difference could be established between the two sides of the partition.

Because Reissner's membrane is difficult to see, especially under strong magnification, a drop of liquid containing very fine silver crystals was dropped on the prepared spot by means of a glass rod (Schmiescheck). If the crystals were of the right size, they sank down upon Reissner's membrane.

When the observations at the apex were concluded, the rubber tube was carefully released from the ring at the round window. Then a slit was made farther along the cochlear lumen, the partition was drilled through at this point, and the scala tympani was closed again with agar and gelatin. Because the bony cochlear axis can be moved with relative ease, especially in its upper part, considerable care had to be taken to avoid lateral pressure on the axis, as the whole spiral would then be distorted.

When pressure was applied, a movement could be observed along the whole cochlea all the way to the stapes. This movement was not just in the basilar membrane, which was dimly visible through Reissner's membrane, but in the partition as a whole (see Fig. 11-72). The partition bent like an elastic rod that was free at one end and fixed at the other. An especially striking phenomenon, which could clearly be established, was that the lower extension of Reissner's membrane moved with almost maximal amplitude.

It was further established that the gelatinous mass in the cochlear duct increased the rigidity of the partition, especially near the helicotrema. For if Reissner's membrane and the gelatinous mass were pushed

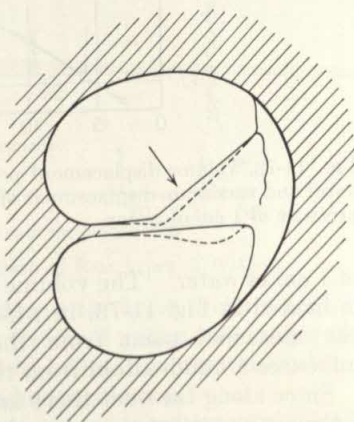


FIG. 11-72. Nature of deformation of the cochlear structures when the stapes was moved inward.

* The mixture consisted of 6 parts of agar, 4.5 parts of gelatin, and 30 parts of water, by weight.

aside (as with a fine brush), the displacement of the basilar membrane at the apex was almost doubled.

The elasticity of the partition is relatively unaffected by other than mechanical factors. Thus, the substitution of tap water for the saline solution in dissection made no apparent difference. Also, when a petrous bone had been kept for two weeks in Lysol solution, the elasticity of its cochlear partition did not differ from that of an entirely fresh specimen.

The applied pressures were chosen to give a maximum displacement at the affected spot of about 0.01 mm. The shape of the area displaced for each pressure was sketched with the aid of a camera lucida, and its surface was measured. In this way the volume displacement was calculated for a length of the cochlear duct of 1 mm under an excess pressure

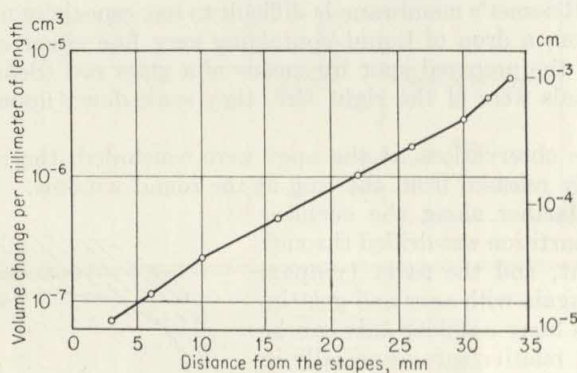


FIG. 11-73. Volume displacement per millimeter of the cochlear duct (left-hand ordinate) and maximum displacement of the cochlear partition (right-hand ordinate) for a pressure of 1 cm of water.

of 1 cm of water. The volume displacements obtained along the duct are indicated in Fig. 11-73, in which the abscissa represents the distance of the measured point from the stapes. As is evident, the elasticity increases a hundredfold from the stapes to the helicotrema.

Since along the duct there are only slight changes in the dimensions of Reissner's membrane and in the form of its displacement under pressure, it follows that the maximum displacement is approximately proportional to the volume displacement. Therefore, by using the right-hand scale of Fig. 11-73, we can find the maximum displacement of the partition for a pressure of 1 cm of water.

Form of Displacement of the Cochlear Partition and Its Relation to the Strength of Audible Undertones. It is a striking phenomenon that a pure tone will generate relatively strong overtones in the ear while no undertones are audible. For example, if we listen to a pure tone of 600 cps, we find no evidence of undertones in the region from 200 to 500 cps even with the aid of a beating test tone and in the absence of significant masking of a lower tone by a higher one.

The existence of such undertones is to be expected on theoretical grounds. If the cochlear partition consists of a membrane that is set into vibration by the pressure changes in the column of fluid above it, it is inevitable that any given strip across the membrane should finally divide into several loops and intermediate nodes when the driving stimulus is made sufficiently great. Correspondingly, with the stapes driven at a given frequency there should be not one but several loci of maximum displacement, the resonant strip closest to the stapes vibrating in its fundamental mode and the more remote points vibrating in upper partials. Such multiple peaks would disturb seriously the mechanical analysis of sound by the cochlea. It is fortunate that the section responding at its fundamental frequency is located nearest to the stapes. Thus, most of the movement of fluid produced by the stapes has been equalized before

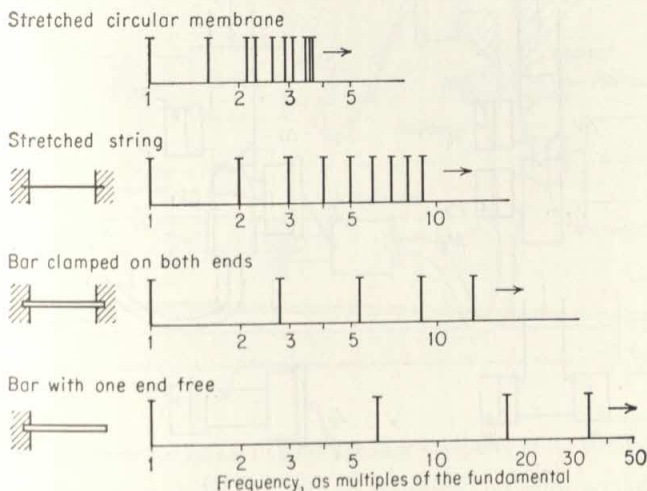


FIG. 11-74. Natural frequencies of vibration of four types of system.

a spot is reached that, if stimulated, would give rise to an undertone. In any case, the important factor in the suppression of undertones is that the locus corresponding to the undertone should be as far along the cochlear duct as possible from the locus of the fundamental tone.

It is well known that the normal frequencies of vibration of different mechanical systems do not show the same distributions. It is important, therefore, to see whether the form of vibration of the cochlear partition suggests a mechanical system having favorable properties in this connection.

On observing the cross section in Fig. 11-72, we see that the deflection of the partition closely resembles that of a bar fixed at one end and whose free end becomes a membrane completing the partition. This type of motion is clearly developed, especially in the turns near the stapes. Now if we consider the normal frequencies exhibited by various vibratory systems expressed as multiples of the fundamental frequency (see Fig. 11-74), it is apparent that, in the case of a bar fixed at one end, the higher

partials are in fact the farthest removed from the fundamental tone. In the cochlear partition the rigidity decreases toward the movable end (of a cross section), for the partition changes from a bony structure into a membrane. This structure, which resembles a bar with one end free and tapering, has characteristic frequencies that are even farther apart than those of a homogeneous bar (Hort and Thoma).

Measurements of Mechanical Impedance for Small Vibratory Systems.

Still another method was used for measuring the elasticity of a membrane that was undergoing extremely small vibrations. The essence of the method lay in using the membrane to close the end of a tube that was transmitting sound. The impedance was determined from the sound pressure at the end of the tube and the volume displacements of the

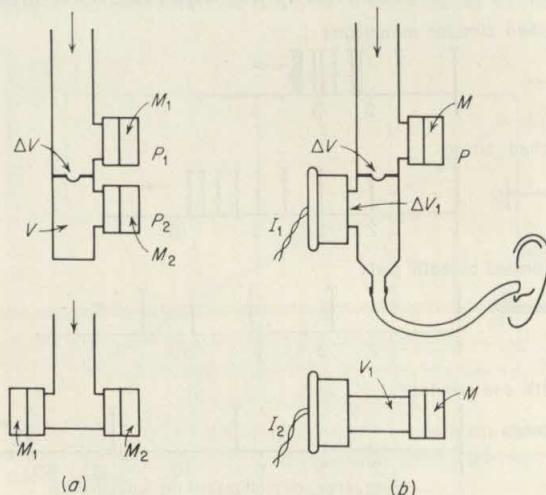


FIG. 11-75. Two methods of measuring the volume displacements of a membrane.

membrane. Two ways of measuring these volume displacements are shown in Fig. 11-75. In the first method, a known small volume V is closed off on one side of the membrane, and the microphone M_2 indicates the pressure changes p_2 arising in volume V as a result of the small volume displacements ΔV of the membrane. Thus, for the impedance, $\Delta V/p = n(V/\rho c^2)(p_2/p_1)$, when ρ is the air density, c the speed of sound in air, and p_1 the sound pressure at the end of the tube as measured with the condenser microphone M_1 . This method presupposes that the elasticity of volume V is much greater than that of the membrane so that it does not decrease the vibrations of the latter. If the two microphones M_1 and M_2 are unequally sensitive so that, when they are attached to a short T tube, microphone M_1 gives an alternating potential n times that of M_2 , then the impedance must be multiplied by n .

In general, the free ear can perceive smaller sound pressures than can be measured with a condenser microphone, because of the limitations of thermal noise. Therefore a second method was used for especially small

volume displacements. In this method, the volume displacement ΔV of the membrane under a sound pressure p was compensated by the volume displacement of the small diaphragm of a telephone receiver. Given a current I_1 to the receiver, if its volume displacement ΔV_1 equals that of the membrane and if the phase is adjusted correctly, nothing can be heard. When the receiver is coupled, by way of a volume V_1 , with the condenser microphone which measures pressure at the end of the

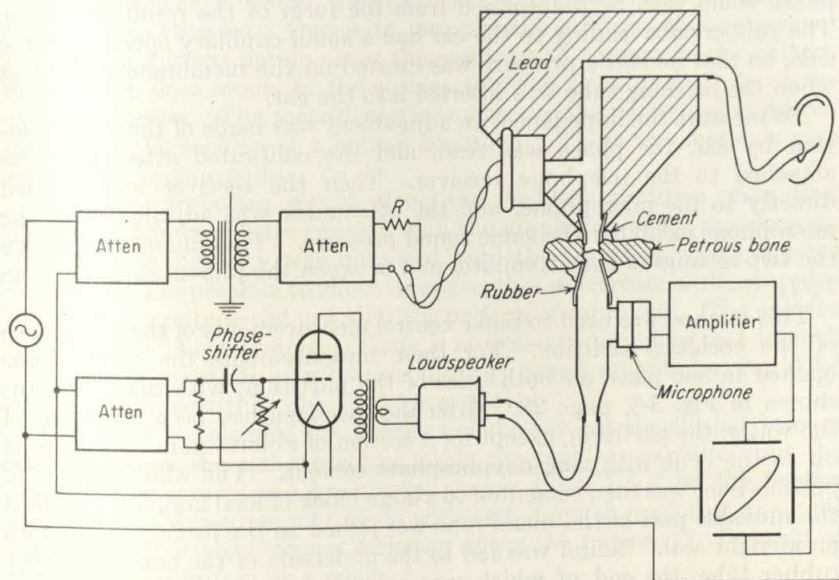


FIG. 11-76. Equipment for measuring the dynamic elasticity of the cochlear partition.

tube, and its current I_2 is adjusted to produce the same sound pressure, the impedance of the membrane can be calculated by the formula,

$$\frac{\Delta V}{p} = \frac{V_1 I_1}{\rho c^2 I_2} \quad (11-1)$$

In this way, the impedance is determined by means of a measurement of volume and the receiver current, which is easily adjustable over a wide range by means of a calibrated attenuator. It is necessary, of course, that the receiver diaphragm have sufficient acoustic stiffness so that its amplitude of vibration will not change when it is coupled with the volume V_1 . This can be ascertained either by listening from the other side of the membrane or by touching the case of the receiver with a wooden stick held between the teeth.

Figure 11-76 shows the complete assembly of the apparatus. The oscillator fed into two calibrated attenuators, of which the upper one was coupled to the telephone receiver by way of a shielded transformer and another calibrated attenuator. (Because current ratios up to 10^6 had to be measured, thorough shielding was necessary.) The lower

calibrated attenuator was connected to the loudspeaker by way of a phase-shifting network. To determine in Eq. (11-1) the reactive component of the membrane impedance as well, a cathode-ray oscillograph was used. The oscillator potential was applied across one pair of oscillographic plates, while the microphone potential, measuring the sound pressure at the end of the tube from the loudspeaker, was applied to the other pair of plates after the acoustic balance had been obtained. The phase could then be determined from the form of the resulting ellipse. The rubber tube leading to the ear had a small capillary opening on the side, so that no static pressure was exerted on the membrane under test when the listening tube was inserted into the ear.

To measure the impedance, an adjustment was made of the compensation by ear, the phase was read, and the calibrated attenuator was attached to the telephone receiver. Then the receiver was coupled directly to the microphone, and the attenuator was adjusted until the microphone exhibited the same sound pressure. The difference between the two settings of the attenuator and between the phases gave the ratio I_1/I_2 .

This method was used to make control measurements of the impedance of the cochlear partition. For these measurements the cochlea was opened in one place on both sides of the partition, with the apparatus shown in Fig. 3-8, page 28. After the specimen had been taken out of the water, the partition, except for a section of about 3 mm, was covered up to the bone with zinc oxyphosphate cement. The whole section of petrous bone was then cemented to a large block of lead in such a way that the movable part of the membrane was joined to the listening tube with an airtight seal. Sound was fed to the underside of the bone through a rubber tube, the end of which was cemented to the bone in the same way.

The values of impedance obtained were somewhat smaller than those from static measurements, probably because the mobility of the partition is somewhat less when a part of it is covered with cement in this way than under normal conditions when it can vibrate freely along its entire length rather than only over a section 3 mm long.

DIRECT OBSERVATION OF THE VIBRATIONS OF THE COCHLEAR PARTITION*

A number of the results reported in this chapter were obtained by direct microscopic observation of the vibrations of the cochlear partition. From time to time, three sorts of criticism of this method have been brought forward. These criticisms are (1) that the amplitude of vibration of the cochlear partition would have to be much larger than normal to permit observation under a microscope, (2) that observations on dead tissues are different from those on living tissues because the mechanical properties change immediately after death, and (3) that the opening in

* Article 66 as listed in the Author's Bibliography. Published in 1952.

the bony wall of the cochlea alters the pattern of vibration within the cochlea. These points will now be considered in detail.

Maximal Amplitude of Vibration in the Cochlea. Experiments carried out on models have made it clear that simply by altering the stiffness of the cochlear partition it may be made to vibrate in various ways, and so may be made to lend support to Ewald's standing-wave theory, to Helmholtz's resonance theory, to the so-called telephone theory, or to various revisions of these theories. There are two ways of deciding among these theories. One is to measure the stiffness of the cochlear partition at various points along the cochlea and to observe the pattern of vibration on a model of the cochlea that has been made to have the same properties. The second way is to observe the pattern of vibration directly in the cochlea of a human specimen. These two methods give exactly the same results.

When the traveling waves along the cochlear partition were first observed, there was little concern with the amplitude of the movements. The stimulus intensity was increased until the traveling waves became visible. It was possible to show, however, that a decrease of the stimulus to half its magnitude did not alter the pattern of vibration. The cochlea therefore is a linear system. There is no reason to suppose that in such a system the pattern of vibration for very small amplitudes would be any different from that observed (page 464).

A study of histological preparations of the ear has shown that intense sounds destroy the cell structures inside the cochlear partition, but the destroyed structures are practically always those lying on the basilar membrane. Measurements made with test hairs showed that the cells are so soft that they do not seriously affect the pattern of vibration of the cochlear partition as a whole.

Observations show that an increase of sound pressure on the eardrum ultimately produces a sensation of pain. If the pressure is increased further the pain increases, but the tonal quality does not change. Therefore it must be assumed that sound pressures near the threshold of pain and even a little above it are still normal physiological stimuli. The sound pressure at the pain threshold is of the order of 3×10^3 dynes per sq cm (page 258). At this pressure the amplitude of vibration of the basilar membrane is about 3×10^{-3} mm for tones between 300 and 1500 cps (page 173). With a microscope with a magnification of 140 times (objective seven times and ocular twenty times) the amplitude of vibration becomes 0.4 mm. The sound pressure and amplitude as given are rms values, but in a microscope the extreme positive and negative positions of the movement are seen, and so the visible vibration is larger by $2\sqrt{2}$. Hence the small silver crystals deposited on the cochlear partition are magnified to lines about 1 mm in length, which is sufficient for observation. In the frequency range from 2000 to 3000 cps the maximal physiological amplitude is about five times larger. There was no need to raise the amplitude above a value that can be tolerated by a normal person, and the measurements were made at that level. The period of observation was always kept as short as possible. In general,

one second was long enough for measurements of the amplitudes of the small silver crystals.

For most of the measurements the stapes was replaced by an artificial stapes. The reason was that the normal stapes rotates about an axis running through its posterior edge, as shown in *a* of Fig. 11-77, because its ligament here is much stiffer than elsewhere. If the middle ear is cleaned out and only the stapes is retained, the stapes can be driven with a vibrating rod attached to a tuning fork or an electromagnetic system. Such a rod vibrates in the direction of its own axis. If the head of the stapes is cemented to the rod the stapes also must perform pistonlike movements. It is no longer able to rotate about its normal axis, and its movement is unphysiological. Under these conditions, sounds producing

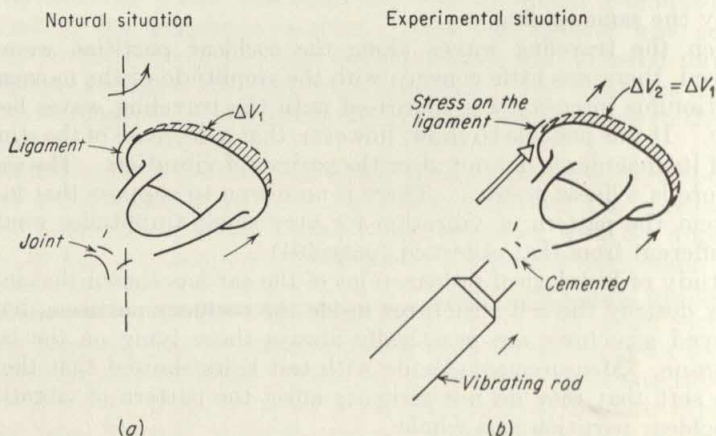


FIG. 11-77. The action of the stapes under normal conditions and when driven by a vibrator.

volume displacements that are still of the order of those normally produced at the threshold of pain can exert an abnormally great force on the posterior end of the stapes. The ligament may be torn here and the stapes pulled away. This injury results because the direction of the forced vibrations is abnormal, and not because the level of the stimulation is excessive. This accident can be avoided by the use of an artificial piston that produces the same volume displacements as the normal action of the stapes, and the effects on the basilar membrane are the same.

Postmortal Changes in the Elastic Properties of Tissues. Most of the purely mechanical measurements that may be carried out on the inner ear are greatly simplified if the ear can be removed from the animal's head and brought into a convenient position. With the compensation technique it is possible to make precise measurements of impedance and to determine the changes of elastic properties in the tissues. In the early experiments on human cadavers it was found that the eardrum is one of the most labile tissues of the ear. After death it immediately

starts to dry out and to increase in stiffness. This change can be prevented by keeping the preparation in a humid atmosphere. When this precaution was taken the average of a group of impedance measurements showed no significant difference from that obtained on living persons.

Disintegration after death continues for many hours, and hence impedance changes will take place over a long period. In fresh human preparations the tensor tendons were severed, and the impedance of the eardrum was measured over a period of 4 hr. The change was less than 1 per cent. Similar experiments were carried out on fresh preparations of calves, which could be made ready for measurements about half an hour after the animal was killed. Over a period of 4 hr it was not possible to detect any change in the position of maximum amplitude of the cochlear partition. This position would have changed if there were an alteration of stiffness of the basilar membrane.

Nevertheless it is obvious that death brings about changes in the cochlear partition. When the cochlear partition of a living guinea pig was observed through a small hole in the bony wall of the cochlea and the guinea pig was then killed by having it breathe pure nitrogen, there were changes in the tissues within 15 min after death. The cells of Hensen and the cells of Claudius became opaque and altered in shape. At the same time there was a decrease in the microphonic potentials. In fact, with experience it is possible to judge the magnitude of the microphonics by looking at the cells. However, these cells are soft in comparison with the ligamentary tissue of the basilar membrane (page 467), and these tissues do not show any changes.

The cochlear partition is about one hundred times stiffer near the stapes than near the helicotrema. This relation holds for man as well as for all the animals investigated, including pigeons, mice, and elephants (page 510). It is this variation in stiffness along the cochlear partition that determines the type of traveling wave. The change in stiffness from one end of the cochlea to the other is so great that a moderate alteration in stiffness in one region would have little effect on the pattern of vibration.

Effect of an Opening in the Cochlear Wall. It seems obvious that a hole in the wall of the cochlea must affect the pattern of vibration along the partition. Many of the early experiments were carried out with a small glass window sealed over the opening in the bony wall. It was found that if the whole preparation was immersed in fluid the glass window could be removed without any significant effect upon the pattern. If there was no fluid above the hole the pattern was altered. A thorough study of a model of the cochlea (page 437) made it clear that the pattern was not changed if the height of the cochlear duct was increased, but it was changed if this height was reduced below the normal value. A hole in the bony wall had the effect of an increase in the height if the hole was covered with fluid.

From the physical point of view this paradox can best be understood by use of the concept of radiant mass for the cochlear partition as suggested by Fletcher (6).

If a hole is drilled in the scala vestibuli, where the fluid movements are generated, the amplitude of the vibrations observed on the basilar membrane may be considerably reduced, but the pattern of the vibration is unchanged. Lowy (2) described an experiment with animals showing that the fluid in the immediate vicinity of the cochlear partition determines the pattern of vibration.

CHAPTER 12

WAVE MOTION IN THE COCHLEA

MECHANICAL PROPERTIES OF THE ORGAN OF CORTI*

It is not difficult to understand why at an earlier time a simple deflection of the basilar membrane was considered to be the stimulus for the auditory nerve fibers in spite of the fact that differentiation in the inner and outer hair cells was known to occur. Then Ranke (2) pointed out the necessity of a duplexity theory of hearing, de Maré arrived at a similar conclusion from fatigue effects, and E. Bárány (2) wrote a review emphasizing the fact that there must be several stimuli acting on the cochlear nerve fibers. Stroboscopic illumination of the organ of Corti during stimulation with a pure tone reveals several varieties of vibrations, all of which change their patterns along the basilar membrane with frequency. Any one of these types of vibrations and displacements could act as a stimulus.

To understand fully the process of hearing it would be necessary to trace each of these types of mechanical vibrations, to discover the corresponding potentials produced in the tissues and nerves, and to study their interactions through inhibition and facilitation. This seems to be a difficult task. For the lateral line of fishes, however, Dijkgraaf was able to show that some of the mechanical stimuli produced by the movements of the fluid surrounding the fish are ineffective and that there are more types of electrophysiological potentials in the tissues than there are forms of behavioral responses. In mammals the depth of anesthesia changes the reciprocal inhibition of the nervous system, hence research in this field is extremely difficult. For every level of anesthesia we shall probably have a different hearing theory.

In the following an attempt is made to describe the different types of vibrations of the organ of Corti during exposure to a pure tone. Each may serve as a mechanical stimulus.

Evolution of the Cochlea. In the evolution of the cochlea there has been a great increase in the length of the basilar membrane. This is shown in a sketchy way in Fig. 12-1 in drawings taken from Hasse. In spite of a marked change in the size of the basilar membrane, there has been practically no change in the shape and size of the vestibular organ.

The finer development of the internal structure of the organ of Corti is shown in the series of cross sections of Fig. 12-2. If we go along the

* Article 67 as listed in the Author's Bibliography. Published in 1953.

line from bird, alligator, and duckbill to man, we can see that each has a basilar membrane, a tectorial membrane, and a Reissner's membrane. The first two structures seem to be important for the transmission of the mechanical stimulus, and Reissner's membrane serves for electrical and chemical insulation of the organ. On the other hand, the hair cells go through a continuous and systematic change. In the bird the hair cells lie in one continuous row beneath the tectorial membrane. There are no pillars to interrupt this continuity. In the alligator, according to Retzius, there are inner hair cells that are clearly differentiable from the outer hair cells. The duckbill has only two rows of inner hair cells separated from the outer hair cells by a space (Pritchard). Finally, in man, there is only one row of inner hair cells around the modiolus, but they are large.

One of the most puzzling features of the cochlear partition of birds is the presence of large blood vessels lying on Reissner's membrane. The slightest movement there should disturb hearing. De Vries

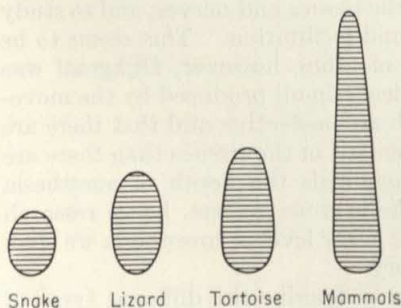


FIG. 12-1. Evolutionary changes in the form of the basilar membrane, after Hasse.

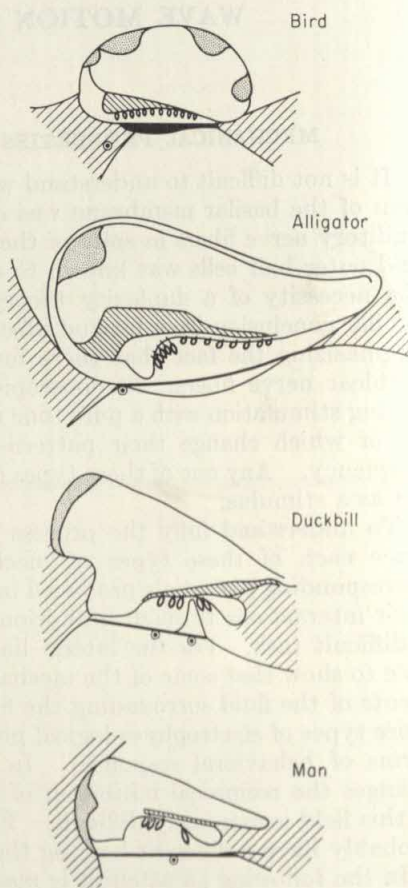


FIG. 12-2. Evolution of the organ of Corti. Blood vessels are contained in the stippled areas.

(1,2) has calculated that even the Brownian movements of the water molecules can play a role in limiting the threshold of hearing. But in birds the red blood cells can be observed under the microscope pushing against the walls of the vessels. As seen in Fig. 12-2, in higher animals and in man the blood vessels are concentrated in the stria vascularis. There they are surrounded by a tough structure, so that dilatations of the vessels produce only small displacements in the endolymph.

In man, the guinea pig, and most other mammals there is one blood vessel, the spiral vessel, running outside the cochlear partition (Fig. 12-3) along the whole length of the basilar membrane. It is symmetrically placed between the inner and the outer hair cells and may supply them by diffusion. If the dilatation has a low frequency so that mass forces are negligible, the displacement of the basilar membrane is considerably less than the dilatation of the vessel. This is so because the stiffness of the basilar membrane is much greater than the stiffness of the tissues covering the vessel, which are formed by loose cells. As seen in the lower drawing of Fig. 12-3, in this case the vessel will be lifted from the basilar membrane according to the ratio of the stiffness on both sides of the vessel.

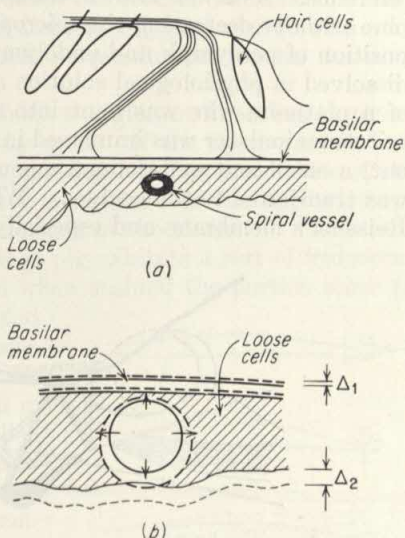


FIG. 12-3. (a) shows the location of the spiral blood vessel; (b) indicates how it expands at each pulse, with a minimum effect (Δ_1) on the basilar membrane.

(3 grams per sq cm on the eardrum at 1.5 cps) for sinusoidal pressure variations at low frequencies (page 258) is probably adapted to the blood pulsations.

Stiffness Pattern of the Organ of Corti. To understand the mechanical performance of the organ of Corti it seems necessary to know something about the stiffnesses of the different tissues. This information can be obtained to a certain degree from microscopic cross sections. By using an adequate staining technique, the fibers and supporting tissues can be differentiated from the softer tissues. A careful summary of work in this field was made by Neubert. The observations show that on the inner side of the basilar membrane there is a triangular fiber network that is connected to the reticular membrane. An upward movement of the basilar membrane produces a radial displacement of the reticular membrane, as shown in the work of ter Kuile and in Fig. 12-4, which shows the organ of Corti of a bat (Zimmermann).

These conclusions were tested on a lightly anesthetized guinea pig. For most of the observations an opening in the bony wall of the cochlea was made near the helicotrema. All observations on the basilar mem-

brane were made at a point about 16 mm from the stapes, except for some control experiments at a distance of 12 mm from the stapes. In a fresh preparation the cochlear partition is practically transparent, and for preliminary observations it is desirable to use intravital staining. In the final observations, when orientation in the cochlear partition was no longer a problem, the slit lamp usually gave satisfactory points of reference. As is well known, the hair cells can be stained with methylene blue without decreasing the microphonics too much. Because the composition of perilymph and endolymph is still not known, the stains were dissolved in physiological solution as concentrated as possible. The tip of a platinum wire was bent into a round loop and with the help of a micromanipulator was immersed in the stain. When the loop was lifted out, a small and well-defined amount of fluid remained in the loop and was transferred to the cochlea. When put into the perilymph it stained Reissner's membrane and especially its nuclei. But after 10 to 15 min,

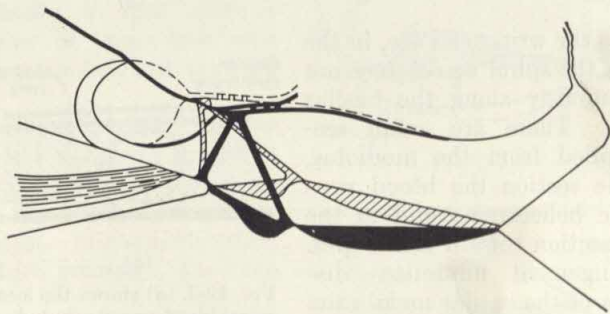


FIG. 12-4. Movements of the organ of Corti of a bat, taken from ter Kuile, after Zimmermann.

the two rows of hair cells appeared a beautiful blue, and Reissner's membrane lost its color so that the hair cells could be observed through an intact Reissner's membrane. The remaining cells were unstained.

When the tissue was stained with methylene blue, it took about 10 to 20 min for the development of the most distinct pictures. After this time the intensity and differentiation between the different tissues decreased. Experience showed, however, that it was possible to slow down all the processes by keeping the animal in air with a low oxygen concentration for several hours before the observations. The animal adjusted itself to this situation, and the microphonics became smaller but remained constant. Then the staining often kept its initial distinctiveness for several hours.

Many other vital stains were tried in the effort to stain the tectorial membrane. Janus green B injected with a micropipette into the endolymph stained this membrane gray-black without staining anything else between Reissner's membrane and the basilar membrane. Later some of the dead cells often began to turn black. This stain made it possible

to observe the vibrations of the tectorial membrane during exposure of the cochlea to sound.

As a general stain, Safranin O was injected into the endolymph. This stain brought out the connective tissues and was used to investigate the reticular membrane.

From a purely mechanical point of view, the organ of Corti looks extremely complicated. Most man-made structures are characterized by some sort of symmetry. But this architecture is similar to an asymmetric crystal with axes that are not perpendicular to one another. This makes the observations difficult.

For a preliminary study of the stiffness in different directions, a pyrex glass needle with a diameter of $5\ \mu$ was used. If the tip was stuck into the tissue and then the needle was displaced parallel to the surface of the tissue, the bending of the needle gave a measure of the applied force necessary to produce a certain displacement of the tissue.

The tectorial membrane of the guinea pig exhibits a sort of iridescent luster under the slit microscope, and when stained the portion close to the helicotrema looks like a flat band lying parallel to the basilar membrane. If an upward force is applied to the outer edge, it curls up, as illustrated in Fig. 12-5. But if the force is applied farther inside the band, the entire band is lifted, and the whole tectorial membrane seems to be rigid. The deformation of the cochlear partition in the longitudinal direction is sketched in the drawing at the bottom of the figure. If the hook that was used to lift the tectorial membrane was suddenly released, it sometimes took the tectorial membrane 1 or 2 sec to return to its original position. If the cells below the tectorial membrane were removed with a hook, then the tectorial membrane remained free of the endolymphatic space. It moved like the cover of a book with the hinge near the modiolus, and

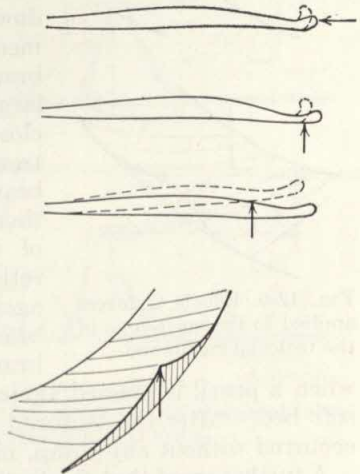


FIG. 12-5. The effect of applying forces to the outer edge of the tectorial membrane.

when it was displaced the return time was always more than a second. The elastic forces in the hinge are small, as in the cupola of the vestibular organ. The tectorial membrane could be split easily along the fibers, which form an angle of about 60° with the edge of the membrane near the modiolus. If two cuts were made close together, a stiff rod was obtained, rotating at the hinge near the modiolus. If a longer section of the tectorial membrane was pulled away from the reticular membrane, it could be bent over and laid on the intact part of the membrane. When released, it took more than 10 sec for the membrane to stretch out. The tectorial membrane is soft and has great

internal friction against slow static deformations. But it seems to be rigid when touched with a needle vibrating at 200 cps. The needle may break the tectorial membrane. The internal consistency of the tectorial membrane has something of the quality of black pitch at a certain temperature. This pitch when laid on the table will spread out slowly over a large area. It seems to be soft. But when hit with a hammer it appears hard and can shatter like glass. The combination of small elastic forces and large frictional forces makes the tectorial membrane stiff with respect to vibrations but lacking in resistive force for slow static displacement.

The tectorial membrane is attached to the reticular membrane. This attachment was observed by cutting a small hole in Reissner's membrane and putting through it a needle with a flat tip at a place close to the outer edge of the tectorial membrane. When the needle was moved slowly downward by means of an automatic arrangement, it was observed that at first the whole organ of Corti was pressed down, but suddenly the edge of the tectorial membrane was lifted from the reticular membrane, in the manner shown in Fig. 12-6. A larger area was lifted when the needle was closer to the modiolus. Near the helicotrema and the modiolus, Reissner's membrane is close to the tectorial membrane. It therefore was possible to lift a long section of the tectorial membrane away from the reticular membrane by pushing a blunt needle against the inner edge of the tectorial membrane, without perforating Reissner's membrane. This effect is similar to that seen

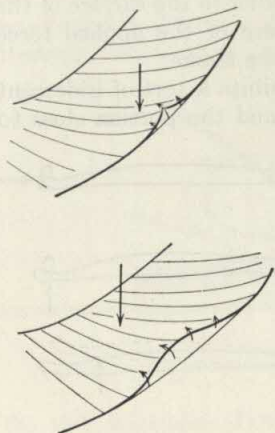


FIG. 12-6. Effects of forces applied to the inner edge of the tectorial membrane.

when a pencil is pressed against the edge of a sheet of paper lying on a soft bed. After the tectorial membrane had been pulled off, the lifting occurred without any jump, in continuous fashion from the beginning.

A further proof that the tectorial membrane is attached to the reticular membrane is that if the needle tip was placed on the cells of Hensen just beyond the outer edge of the tectorial membrane and was slowly moved down, the tectorial membrane followed this movement. When it was lifted by the method described above, its attachment was loosened.

After the tectorial membrane had been torn away, the next step was to investigate the reticular membrane. It was possible to confirm the fact that the reticular membrane represents a stiff covering plate in which the hair cells are fitted on one end and hang down practically free at the other end. Furthermore, the reticular membrane is rigidly attached to the basilar membrane by two pillars, as shown in Fig. 12-4.

A crude way to test the relative rigidity of different layers is to observe the impression produced by a dull needle on the surface. If the impression produced for a given penetration below the surface does not spread

greatly in a lateral direction, then the tissues under the needle are soft. For a cover plate lying on a soft bed the lateral spread of the deformation is large. In Fig. 12-7 the deformation of the surface along the longitudinal axis of the cochlear partition is shown in a schematic way when a needle with a flat tip and a diameter of $5\ \mu$ is impressed on the surface of *a*, Reissner's membrane (a simple parallel displacement), *b*, the normal organ of Corti with the tectorial membrane, *c*, the reticular membrane after the tectorial membrane has been pulled off, *d*, the cells of Hensen, and *e*, the basilar membrane. When the needle was moved up and down several times and was displaced at the same time from the outside toward

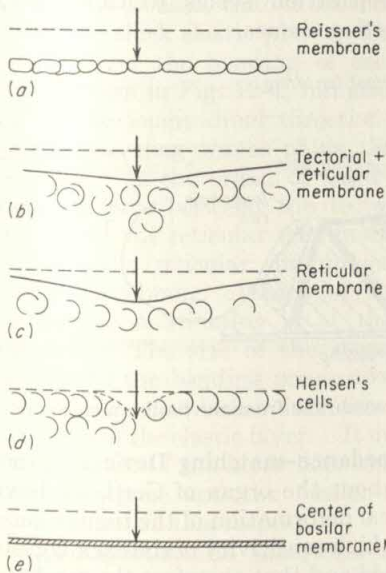


FIG. 12-7. Effects of applying a flat-tipped needle to various structures of the organ of Corti.

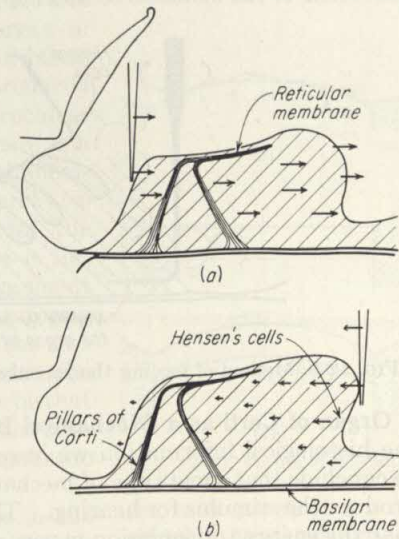


FIG. 12-8. Effect of a force applied laterally to the pillars of Corti.

the modiolus, it was striking to see that the soft penetration of the cells of Hensen stopped when the edge of the reticular membrane was reached, giving the definite impression of a stiff cover lying on a soft bed.

After the tectorial membrane has been removed the remaining pad on the basilar membrane is much stiffer with respect to radial displacement near the modiolus than on the side of the cells of Hensen. Figure 12-8 shows that the inner side of the pad is mechanically attached to the reticular membrane, and therefore the whole organ of Corti moves outward with the same size of displacement if a lateral force is applied, because the reticular membrane pulls the organ along with it. But if the lateral pressure is applied to the cells of Hensen, which are soft, the stiff pillars of Corti on the inside are only slightly displaced.

It was possible to loosen the organ of Corti from the basilar membrane by undercutting it with a rectangularly bent needle. When the reticular membrane was lifted slightly, the hair cells were seen hanging on the reticular membrane (Fig. 12-9).

With needle tips smaller than $5\ \mu$ the reticular membrane can be perforated easily, but not the tectorial membrane or the basilar membrane. Mechanically, the reticular membrane seems to be a type of net. Once perforated, its stiffnesses against movements along the surface of the membrane are about the same in the radial and longitudinal directions, and they are very large. All observations *in situ* on a living guinea pig were in agreement with the conclusions reached from a study of histological sections. The histological preparation seems to cause little distortion of the connective and supporting tissues.

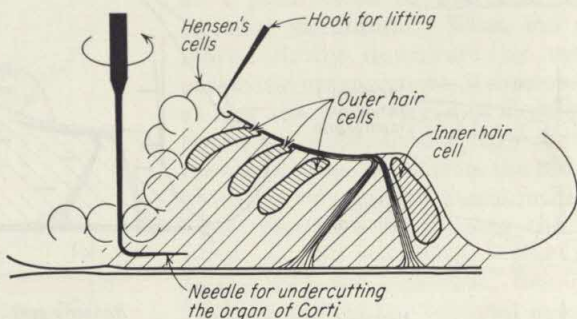


FIG. 12-9. Method of freeing the reticular membrane from the basilar membrane.

Organ of Corti as a Mechanical Impedance-matching Device. From the histological information we have about the organ of Corti, we have to conclude that some type of mechanical deformation of the tissues must produce the stimulus for hearing. The high sensitivity of the ear suggests that the energy transmission is very good and that therefore the mechanical impedances must be matched. There is a big gap in impedance between the air and the elastic tissues of the organ of Corti. The eardrum and ossicles of the middle ear overcome the gap partially by matching the impedance of the air to the mechanical impedance of the vibrating fluid columns in the perilymph and the elasticity of the cochlear partition. These movements of the perilymph are displacements of the fluid. In order to pick up the energy of these fluid movements and transfer it to the stiffer elastic tissues, a second match of the impedances is needed, which transforms the pressure acting on the basilar membrane into a larger force. In Fig. 12-10 three different types of matching devices are shown: *a* represents a lever that transforms the small force *f* into a larger force *F*. No loss of energy is involved in the transformation, and the displacement of force *f* therefore is larger than the displacement of force *F*. From *b* it can be seen that a relatively small pressure on a membrane can produce large tangential stresses in the membrane and its enclosing frame. As a matter of fact, if the membrane is a plane,

any pressure on one side of the membrane would produce an infinitely large tension on the frame. A pressure on an elastic membrane can be transformed not only into a pull but also into a shearing force. This is shown in drawing *c*, where a part of the surface of an elastic plate is covered with a thin layer of stiff material. Bending the plate produces under the stiff layer shearing forces that may be large compared with the pressure forces used for the bending of the plate.

In the organ of Corti it seems that, of the three schemes shown in Fig. 12-10, the last one, *c*, is used, that of an inelastic thin layer on a thick elastic plate. This is valid not only for the bending of the organ of Corti, shown in Fig. 12-4, but also for bending in the longitudinal direction produced by the traveling waves along the cochlear partition. In the organ of Corti there is a shearing force between the tectorial membrane and the reticular membrane and also between the reticular membrane and the basilar membrane. Which of these is important as a stimulus is at the moment unknown. The size of the shearing forces relative to the bending pressure on the surface of the membrane increases with the thickness of the elastic layer. It may be that the thickness of the layer between the reticular membrane and the basilar membrane is important in this respect.

The importance of shearing forces in the vestibular organ has been pointed out by J. Breuer and proved in outstanding experiments by Holst. Shearing forces in the cochlea were proposed by ter Kuile.

Resonant Systems and Traveling Waves. At the moment there seem to be two methods of investigating the vibratory pattern of the organ of Corti. One is a direct microscopic observation of the cells during stimulation by a sound, and the second is the technique of picking up microphonics from different points with a search electrode, as has been done by Tasaki, Davis, and Legoux. The use of microphonics has the advantage of being a more sensitive method. It has the disadvantage that at the end a microscope is still needed to locate the place from which the microphonics are picked up. A further difficulty is that if we stick the electrode into the cells, we need an electrode that has no relative displacement toward the cells. Otherwise the electrode picks up both the microphonics of the deformation through the sound and the deformation produced by the relative displacement between tissue and electrode. If

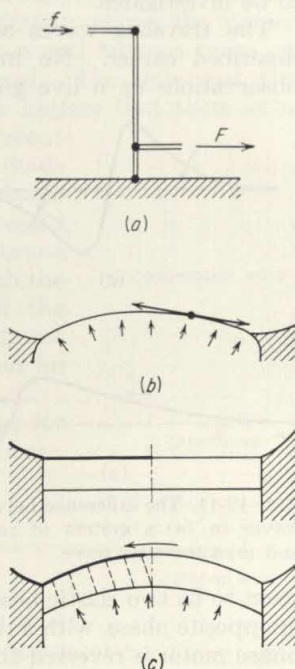


FIG. 12-10. Forms of mechanical impedance matching. (a) the lever principle; (b) the stretched membrane principle; (c) a shearing action.

we place the electrode in the surrounding fluid, the microphonics of the relative movement between cell and electrode are largely reduced, but we are to some extent observing a scattered electric field because the organ of Corti has several electrically insulating layers whose positions have still to be investigated.

The traveling waves along the cochlear partition as a whole were described earlier. No important differences were found between the observations on a live guinea pig and on one that was dead for 3 hr.

But it is still possible that inside the organ of Corti there are some membranes or a row of fibers that could show vibrations according to the resonance theory. This can be investigated with a stroboscope.

When we have a row of simple resonant elements with increasing resonance frequencies placed along a horizontal line, as in the Frahm reed frequency meter, a constant sinusoidal force acting on the elements shows under stroboscopic illumination a displacement of the form *a* in Fig. 12-11. The over-all movement on both sides of the resonance frequency is purely transverse. There

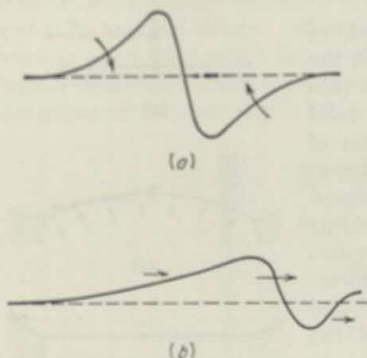


FIG. 12-11. The difference between the waves in (a) a system of resonators and (b) a traveling wave.

seem to be two elastic beams on both sides bending up and down, always in opposite phase, with a thread of higher elasticity between them. If the phase motor is reversed the picture does not change.

Very different from this is the stroboscopic picture of a traveling wave. The main impression is of a movement along the horizontal axis (Fig. 12-11b). Even in a small section of the traveling wave this movement can easily be recognized. The reversal of the phase motor reverses the direction of the horizontal movements. The difference between the two pictures is so great that even in a small section they can always be discriminated. No structure along the cochlear partition showed movements corresponding to a system of resonant elements of the kind seen in a Frahm reed frequency meter.

Under the microscope a vibrating needle was used to touch surfaces, membranes, threads, gelatinous paddings, beams, and all other types of material. It was surprising that there were always traveling waves running toward the needle or away from it, according to the direction of rotation of the phase motor. A resonance phenomenon as described in the textbooks can only be obtained if the elastic and mass forces in a system are clearly separated as in a pendulum. But even in a pendulum there are difficulties, because when pushed in one direction the bob does not keep swinging in the same plane but transfers its energy from one degree of freedom to a second degree of freedom. Physically it is hard to avoid coupling between the two degrees of freedom. If there are two

resonant systems with coupling between them, an exchange of energy between the two cannot be prevented. If there are several coupled resonant systems, the energy will travel around more and more, which for a large number of resonating systems gives a traveling wave. As a matter of fact, if a rubber pad is pressed against the stems of the vibrating rods in the Frahm frequency meter immediately above the pattern shown in Fig. 12-11a, a traveling wave appears and becomes more and more pronounced as the coupling is increased. The statement that there are no traveling waves in the cochlea implies that there is no elastic or frictional coupling between the different segments of the basilar membrane and the fluids that load these segments. If there is no elastic coupling between the segments, a needle pressed against the organ of Corti or the basilar membrane should produce a thin elliptical impression with the longer axis lying in the radial direction of the cochlea. But the experiments showed an almost round impression similar to that obtained on an elastic plate.

It is known that the differential equations for transverse movements of strings, membranes, bars, and pads have the form

$$\frac{\partial^2 y}{\partial x^2} = \frac{1}{c^2} \frac{\partial^2 y}{\partial t^2} \quad \text{or} \quad \frac{\partial^4 y}{\partial x^4} = \frac{1}{c} \frac{\partial^2 y}{\partial t^2}$$

where y is the transverse displacement, t the time, and x the longitudinal axis. The solution of these equations is of the form

$$y = Ce^{2\pi i(\mu x - \nu t)}$$

which represents a traveling wave along the x axis. It appears that in some theoretical speculations this fact has not been taken into consideration sufficiently. It is useful to study long-distance telephone lines, for they introduce the wave and resonance concepts at the same time.

Unfortunately, the waves in elastic bodies are complicated, and, as with earthquake waves, several problems still await solution. Tasaki, Davis, and Legoux discussed the different waves in the cochlea. As shown by Berger (1,2) in Fig. 12-12, five different waves can be discriminated: (1) compression waves, (2) shear waves, (3) dilatation waves, (4) Rayleigh waves, and (5) bending waves. The problem of the next section will be to find out whether some of these can be recognized in the elongated organ of Corti.

The wave velocities of all these waves are different for the same medium. Even in a rectangular bar, when the thickness is different



FIG. 12-12. Possible forms of traveling waves.

from the width, the transverse vibrations in the perpendicular direction have different traveling velocities, which produce a vibratory pattern that is hard to keep in mind. Theories of how the nerves are stimulated by the displacements in the cochlea were presented by Huggins and Licklider.

Stroboscopic Observations of the Organ of Corti of a Guinea Pig. When the vibrating cochlear partition was first seen the whole organ of Corti seemed to be moving up and down in phase with the basilar membrane. It was necessary to consider more closely the displacements of the different tissues relative to the basilar membrane. These relative displacements are to a large degree in the plane of the basilar membrane. The opening in the cochlea was always closed with a glass window and fixed so that it did not show any movements. Otherwise, the movement of the air-perilymph boundary as seen through the microscope might be mistaken for movements of the organ of Corti.

Most of the observations were made close to the helicotrema, about 16 mm away from the stapes. But the same type of results were obtained at a distance of 12 mm from the stapes.

In an intact cochlear partition, Reissner's membrane moved up and down with the same phase along the visible surface if the frequency was low. But for higher frequencies, *e.g.*, 1000 cps, small bending waves (Fig. 12-12) traveled in the longitudinal and radial directions of the cochlear partition, as may be seen on any loose membrane. In order to find out further what the possible free vibrations of the different parts of the organ of Corti might be, an effort was made to separate the different tissues. A longitudinal cut made by a needle along the outer edge of the reticular membrane separated the cells of Hensen from the outer phalangeal cells, so that the cells of Hensen stood free on the basilar membrane. If a low-frequency tone was used to set the basilar membrane into vibration, these cells were compressed and dilated in the longitudinal direction, showing a dilatation wave like (3) of Fig. 12-12. If the cells were partially cut away from the basilar membrane, this type of movement was even more pronounced. The cells of Hensen are very soft, and the wavelength for 500 cps is about as long as the thickness of the pad formed by the cells. If the tectorial membrane was lifted from the reticular membrane so that it stood free in the endolymph, it was surprisingly stiff against vibrations, and no wave motion could be seen on it.

As can be seen from Fig. 12-13*a*, the outer leg of the pillars of Corti may produce a local load on the basilar membrane, and this in turn may facilitate a subdividing of the basilar membrane (Fig. 12-13*b*) for high frequencies. When the point of maximal transverse vibrations along the basilar membrane was observed and the frequency was increased three times, no subdivision of the basilar membrane in the radial direction could be found, but there remained a small phase difference between the center and the edge of the membrane. From this observation comes the theoretically important conclusion that the mechanical load concentrated at one point of the basilar membrane by the pillar of Corti is relatively small compared with the load of the surrounding fluid.

If the different tissues were loosely coupled with each other, the cells of Hensen would keep their longitudinal vibrations and the basilar membrane its transverse vibration. But the intact cochlear partition gives the impression that the coupling is strong, and at first it seems that the movements of the basilar membrane are the primary ones and that the reticular membrane joins with these movements in a passive way as they are conveyed through the pillars of Corti and the cells of Hensen. The stiff tectorial membrane is loosely attached to the reticular membrane and damps its vibrations. Reissner's membrane has the loosest coupling to the vibrations of the basilar membrane, but by observing the stained nuclei of its cells it is easy to see that the longitudinal and radial displacements of the cells of Hensen are transmitted even to this membrane.

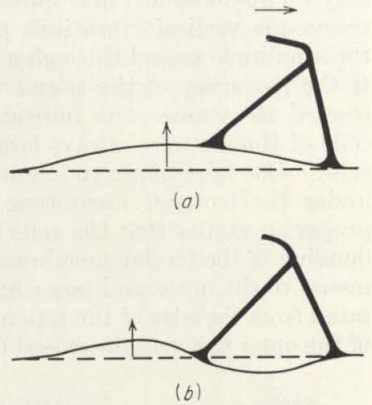


FIG. 12-13. Possible forms of displacement of the basilar membrane.

By looking through Reissner's membrane at the organ of Corti, the following vibrations relative to the basilar membrane could be seen

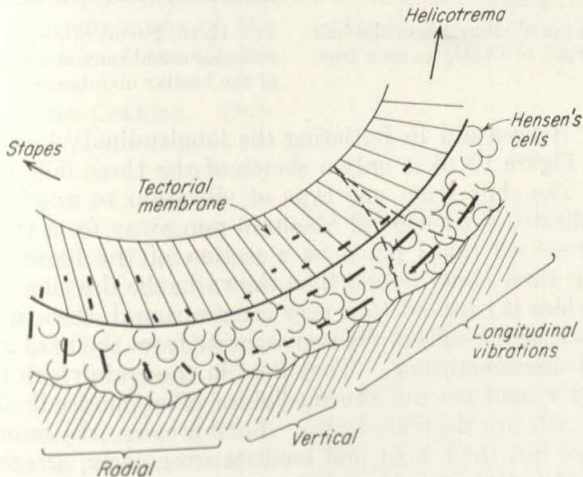


FIG. 12-14. The distribution of radial and longitudinal vibrations along the organ of Corti during tonal stimulation. The view was through Reissner's membrane.

(Fig. 12-14) near the place of maximal transverse vibrations of the basilar membrane. On the side of the stapes the ends of the hair cells under the tectorial membrane and the cells of Hensen executed vibrations in a direction close to the direction of the fibers of the tectorial membrane. This type of vibration was in close agreement with the displacements

shown in Fig. 12-14. As the helicotrema was approached this type of vibration stopped suddenly, and the inner and outer hair cells showed only an up-and-down movement. Farther in the direction of the helicotrema the vertical vibrations passed over into longitudinal vibrations, the amplitude passed through a peak, and then everything quieted down. If the frequency of the sound was increased, the whole pattern moved toward the stapes. As indicated in Fig. 12-14 the movements of the cells of Hensen were always larger than the movements of the outer hair cells. But in response to longitudinal vibrations the tip of the hair cells under the tectorial membrane was so greatly damped that it seems proper to assume that the cells of Hensen are moved by the longitudinal bending of the basilar membrane, and they in turn transmit their movements to the outer and inner hair cells. When the hair cells were separated from the edge of the reticular membrane the longitudinal vibrations of the outer hair cells decreased their amplitude to one-fourth. Therefore

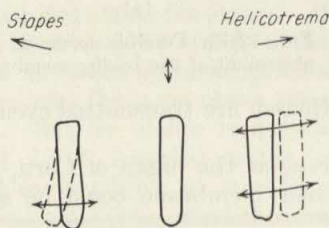


FIG. 12-15. Types of vibration of the hair cells in the organ of Corti, as seen from one side.

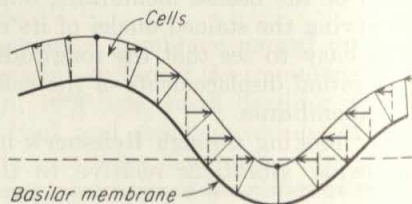


FIG. 12-16. Forms of displacement of the reticular membrane caused by movement of the basilar membrane.

the cells of Hensen aid in initiating the longitudinal vibrations of the hair cells. Figure 12-14 is only a sketch of the three different types of vibration. The shift from one type of vibration to another is not as sharp as indicated. At a point about 16 mm away from the stapes the change represented takes place on a section of the basilar membrane that is about three times longer than shown in the drawing.

If the cochlea is exposed to a very intense sound, then in general the first event is that the cells of Hensen separate from the basilar membrane and the reticular membrane. They float in the endolymph freely like a thick thread wound around the modiolus. The longitudinal vibrations of the hair cells are decreased also. Furthermore, the outer hair cells seem to have lost their hold and oscillate irregularly, attached only at the upper end to the reticular membrane.

On looking at the organ of Corti in a radial direction, so that the whole length of the hair cells can be seen, the outer hair cells seem to oscillate, as shown in Fig. 12-15. Toward the stapes, the lower end of the hair cells oscillates slightly in the longitudinal direction. It was not possible to find out whether the cells are bent or only rotated. But on the side of the helicotrema the outer hair cells undergo a simple parallel displacement. The movements shown in the figure are displacements relative

to the basilar membrane, so that its up-and-down movements have to be added.

At first it is surprising to find that the hair cells vibrate in the longitudinal direction of the basilar membrane. But the hair cells in mammals are located high above the basilar membrane. Therefore, if the basilar membrane is bent along the longitudinal displacement axis, as shown in Fig. 12-16, a longitudinal displacement occurs. The amplitude of this displacement is proportional to the vertical amplitudes of the basilar membrane and the first derivative of the momentary position of the traveling wave along the basilar membrane. The shape of the traveling wave along a human basilar membrane for a tone of 200 cps is shown in Fig. 12-17 as the curve $f(x)$ (see page 462). The integral and the first and second derivatives of the curve are shown also. The maximum of the first derivative $f'(x)$, represented by the envelope and responsible for the size of the longitudinal vibrations, is displaced toward the helicotrema relative to the maximum of the vertical vibrations $f(x)$ of the basilar membrane.

Curvature of the Cochlea. During the evolution of the cochlea the basilar membrane is continuously lengthened (Fig. 12-1), but at the same time it starts to curve. In birds and in the duckbill the curvature is bow-shaped, but in the guinea pig four turns can be seen. The question is raised whether the turns have any purpose. It is obvious that the blood and nerve supply to a coiled organ of Corti are better isolated and protected in a central shaft like the modiolus than would be possible if the organ of Corti were a long stretched pad exposed to mechanical bending. But, in addition, the curvature may be necessary to the proper working of the organ of Corti.

For instance, the tectorial membrane is connected by a hinge to the inner side of the bony wall of the cochlea. In this way the tectorial membrane is relatively loose for up-and-down movements. If the

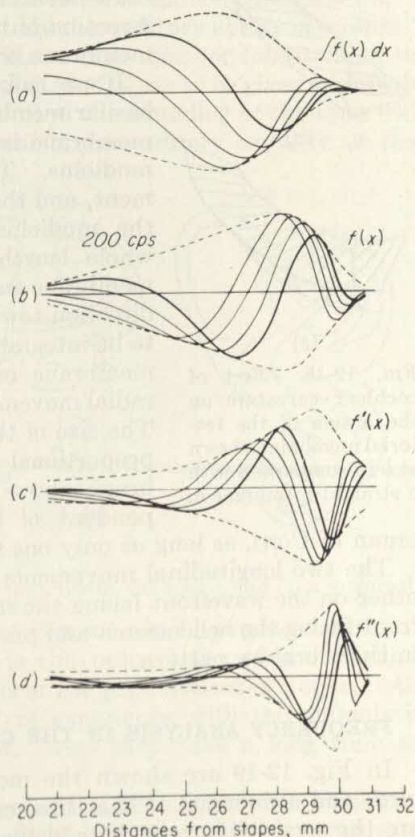


FIG. 12-17. Traveling waves along the basilar membrane produced by 200 cps. Shown are the displacement wave (b), its integral (a), and the first two differentials (c) and (d).

cochlea were straight, as in Fig. 12-18*a*, a pull at one place would bend the whole tectorial membrane like a book cover, and displacements would be transmitted along the entire length. With a coiled cochlea the tectorial membrane bends down only as far as the nearest corner (Fig. 12-18*b*). Figures 12-18*a* and *b* are exaggerated, but the effect in the cochlea can be seen. It is more pronounced for a loose hinge, and the peculiar striated texture of the tectorial membrane seems to limit deformation, especially in the direction of the helicotrema, because the tectorial membrane breaks when the cochlea is coiled.

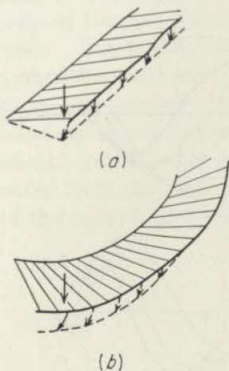


FIG. 12-18. Effect of cochlear curvature on the action of the tectorial membrane, shown at *b* in comparison with a straight membrane *a*.

If we look at Fig. 12-4 we can see that if the basilar membrane is moving upward the reticular membrane is displaced toward the center of the modiolus. The cells of Hensen join in this movement, and therefore the radius of the circle around the modiolus is decreased. This decreases the whole length of the elastic pad on the basilar membrane and produces a push in the longitudinal direction toward the helicotrema. This push has to be integrated over a longer section of the basilar membrane on the side of the stapes where the radial movements of the reticular membrane occur. The size of the longitudinal displacement is again proportional to the height of the reticular membrane above the basilar membrane. It is independent of the radius of the curvature of the

organ of Corti, as long as only one turn is taken into consideration.

The two longitudinal movements described may compensate for each other on the wavefront facing the stapes and add together on the wavefront facing the helicotrema and produce in this way the sharp transition in the vibratory pattern.

FREQUENCY ANALYSIS IN THE COCHLEAS OF VARIOUS ANIMALS*

In Fig. 12-19 are shown the membranous labyrinths of a turtle, a bird, and a mammal. The three canals at right angles to one another are the semicircular canals, which serve for determining the position of the head. The areas enclosed by dotted lines represent small otolithic organs which also serve for equilibrium. The auditory nerve ends in the regions indicated by crosshatching, and therefore these regions serve for hearing.

In these three stages of development of the membranous labyrinth it is apparent that the semicircular canals undergo practically no change that is externally obvious, whereas there is a progressive change in the length of the basilar membrane, as represented in the crosshatched region. This increase in length causes the lowermost otolith to be displaced to

* Article 45 as listed in the Author's Bibliography. Published in 1944.

the end of a tube, until in the mammalian labyrinth it completely disappears.

The question now arises to what extent the auditory ability of various animals is improved by this increase in length of the basilar membrane, and indeed whether there is any improvement at all. It is especially of interest whether this increase of length only results in an extension of the auditory range for low and high tones, or whether it gives an improvement in the ear's ability to discriminate tones of different frequencies.

Many methods have been used to study the auditory ability of animals, as Kleinknecht has pointed out. Thus a test tone (or food tone) can always be presented simultaneously with food, so as to be given a biological value to the animal. After a few days the sounding of the tone will then evoke certain movements by which the auditory capacity of the animal can be judged.

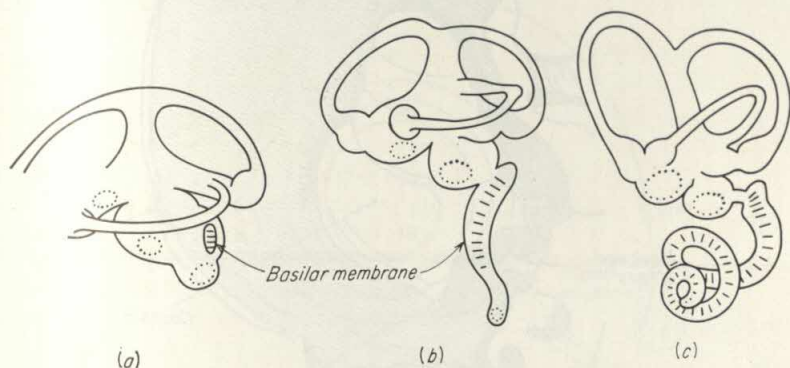


FIG. 12-19. The membranous labyrinths of (a) a turtle, (b) a bird, and (c) a mammal.

In certain instances also a reflex movement can be produced without training. Particularly well known is the pinna reflex of guinea pigs, which consists of a twitch of the pinna at the presentation of a tone. All these methods require a great deal of experience with the animals if erroneous results are to be avoided. Also they take a long time to carry out.

It is simpler to use the electrical potentials that arise in the region of the basilar membrane (Wever-Bray effect) or in the auditory nerve as a result of stimulation by sounds. In this way the auditory threshold is readily determined as a function of frequency. The potential changes caused by beats may be observed in the higher portions of the nerve tract, and information may be obtained on frequency discrimination also.

In all these situations, however, the mechanical form of frequency analysis is connected with the neural form, so that no certain picture is obtained of the effectiveness of the length of the basilar membrane. Therefore a purely anatomical way of investigating the ear's mechanical analysis was attempted.

It has been found possible in man to make direct measurements of the amplitude variations along the basilar membrane for various frequencies

(page 448). Therefore it seems possible to discover the frequency range within which any change of frequency produces a change of position of the response of the cochlear partition. In this way every region of frequency within which a mechanical analysis occurs can be specified relative to the lower limit of hearing. The upper limit of resolution cannot be determined because the vibratory amplitudes for the high tones are too small to measure. The cochleas of various animals were studied in this way.

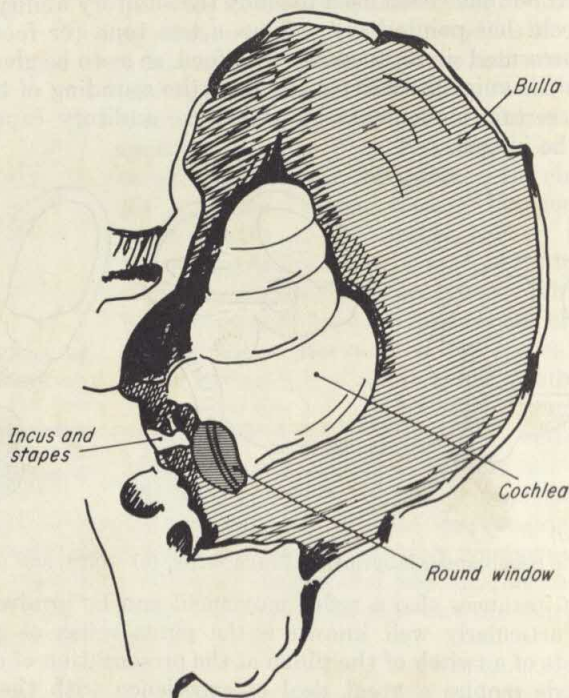


FIG. 12-20. The guinea pig's cochlea.

The Guinea Pig. When a comparison was made of the anatomical structure of the cochleas of various animals, only small differences were found in the magnitudes of the fluid streaming in the cochlea. On the other hand, there are large variations in the external structure of the cochlea. In man the whole cochlea is embedded in hard bone, whereas in the guinea pig and most rodents the cochlea consists of a thin shell of bone standing free in a large bony cavity. This towerlike form for the guinea pig is illustrated in Fig. 12-20. The internal structure of the cochlea shines through the shell, so that four complete turns can be made out. As man has only $2\frac{3}{4}$ turns, the question arises whether any higher stage of development has been reached.

The stapes here consists of a knob with a straight rod, as the figure shows.

The thin-walled cochlear capsule cannot be opened with a drill because its limited strength permits a large portion to be broken in. Either the wall has to be strengthened with zinc oxyphosphate cement, or a small portion of the wall is penetrated with a sharp needle or forceps. This last method has the advantage that the location of the cochlear partition is easily seen from the outside.

In order to measure the vibratory characteristics of the cochlear partition it is necessary to construct a diagram of the cochlea for every species of animal. Such a diagram is drawn for the guinea pig in Fig. 12-21, with the points of maximum bulging of the cochlear partition shown as projected upon a plane perpendicular to the vertical axis. Also shown are the distances along the cochlear partition as measured from

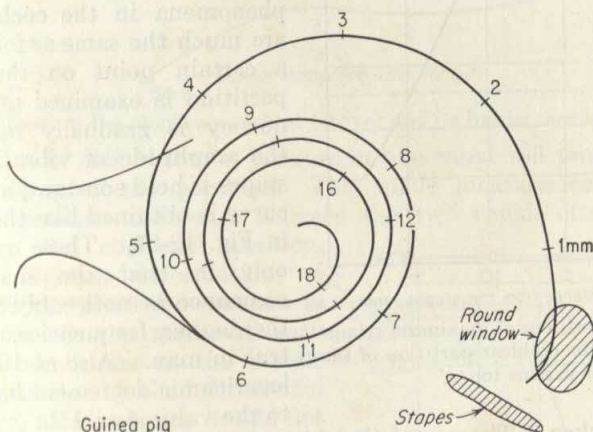


FIG. 12-21. Spiral diagram of the cochlear partition of the guinea pig. The numbers indicate distances from the stapes.

its basal end near the stapes. The two crosshatched areas represent the positions of the round window and oval window. The oval window is covered by the stapes.

The length of the guinea pig cochlea is only 18 mm, whereas man's is 35 mm. From this we may conclude that in spite of its larger number of turns the guinea pig can achieve a spatial separation of tones over the cochlear partition only in the upper region of the frequency scale. This conclusion can be established only if for every position along the cochlea a frequency can be found for which the cochlear partition undergoes maximum vibrations. In these determinations the volume displacement of the stapes was kept the same for all frequencies.

The results of these measurements are given in Fig. 12-22. At a frequency of 200 cps the maximum vibration of the cochlear partition reaches a position farthest from the stapes, and a further lowering of the tonal frequency produces no change in the form of vibration. The amplitude becomes smaller because more and more of the fluid motion is

equalized through the helicotrema. Therefore a mechanical analysis below 200 cps cannot take place in the guinea pig cochlea.

Though there may not be any mechanical frequency analysis below 200 cps, it is still possible that a frequency analysis of limited form can occur through neural processes. Then the difference threshold will be significantly larger for the region below 200 cps. The same relations ought to hold for hearing as for the vibratory sensitivity of the skin, which shows only limited frequency discrimination.

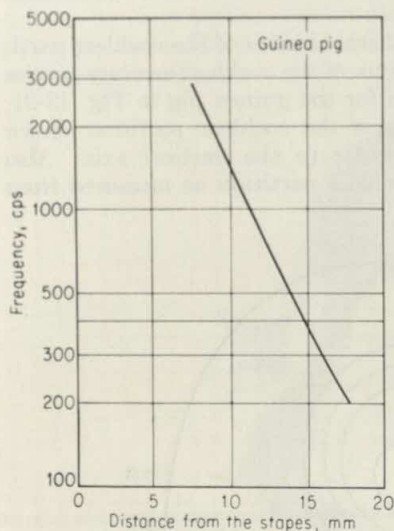


FIG. 12-22. Positions of maximum stimulation along the cochlear partition of the guinea pig for various tones.

In other respects the vibratory phenomena in the cochlear canal are much the same as for man. If a certain point on the cochlear partition is examined and the frequency is gradually raised while the amplitude of vibration of the stapes is held constant, a resonance curve is obtained like those shown in Fig. 12-23. These curves vary only in that the sharpness of resonance is noticeably greater at the higher frequencies, just as is true in man. Also at 1000 cps the logarithmic decrement has declined to the value $\delta = 1.2$.

The Chicken. The ear of the chicken seems to have reached only an early stage of development. Its cochlea consists of a weakly bent tube about 5 mm long.

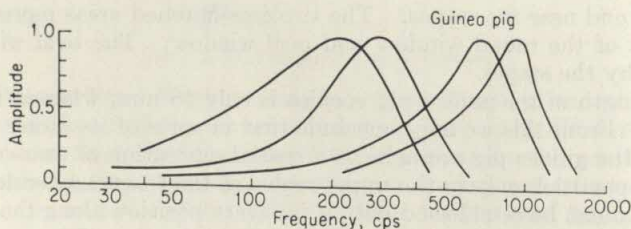


FIG. 12-23. Resonance curves for the cochlear partition of the guinea pig, at four positions.

The development of the cochlea thus seems to begin with an elongated sac of the membranous labyrinth that is embedded in a bony canal and that has loosened itself from the bony wall all along one side. Thus there arises in a bony tube a second tube with an elastic wall, *i.e.*, a double canal with an elastic partition. In the chicken the elongated sac

is still closed at the end, so that there is no connection between the two canals corresponding to the helicotrema of man.

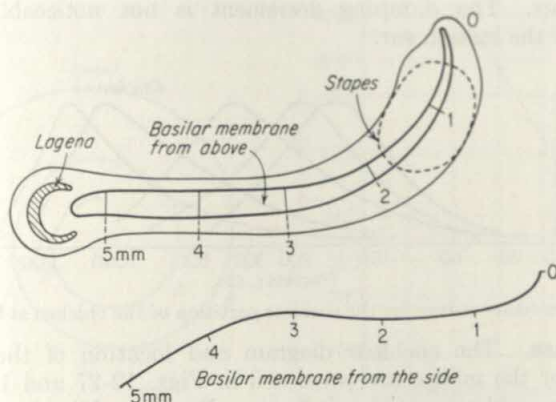


FIG. 12-24. Form of the chicken's cochlea (above) and its basilar membrane (below).

The result of this is that a pressure in one canal will produce a persistent bulging of the partition. This made measurements difficult, because a pressure difference between the two canals often caused a tearing of the cochlear partition. Also the slightest deformations of the middle ear produced changes in the cochlea. In the mammals such incidental conditions of the middle ear were canceled by the helicotrema.

However, a helicotrema would not be advantageous in birds. Because of the limited length of its cochlear canal an opening would greatly reduce the ear's sensitivity.

In Fig. 12-24 the basilar membrane of a chicken is represented as seen from above and somewhat from the side. At the end of the basilar membrane is a white calcium deposit. The location of the stapedial footplate in relation to the double canal is shown by the dotted line.

The shifting of the positions of resonance along the cochlear partition with changes of frequency are shown in Fig. 12-25. Below 100 cps there is no longer any mechanical frequency analysis in the chicken, because the cochlear partition vibrates as a whole, and this form of vibration is unaltered as the frequency is made lower. The upper limit of the auditory range can be obtained by extrapolation to zero length of the membrane in this figure.

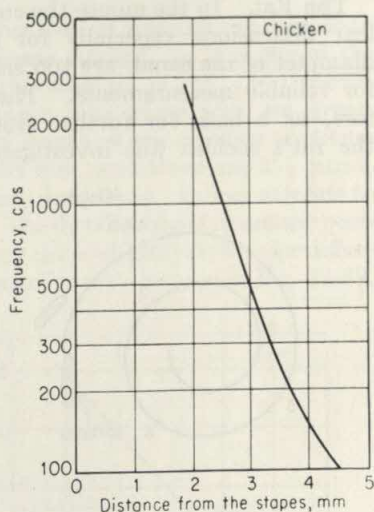


FIG. 12-25. Positions of maximum stimulation along the cochlear partition of the chicken for various tones.

It is of special interest whether the resonance curves change in a cochlear canal as short as this one. Figure 12-26 gives results of the measurements. The damping decrement is not noticeably different from that of the human ear.

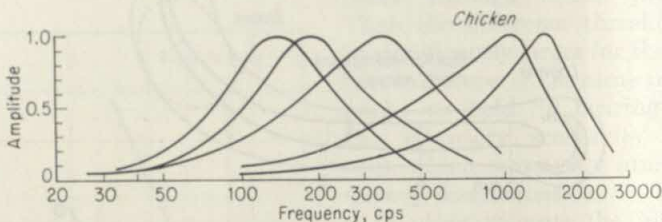


FIG. 12-26. Resonance curves for the cochlear partition of the chicken at five positions.

The Mouse. The cochlear diagram and location of the places of resonance for the mouse are presented in Figs. 12-27 and 12-28. The length of the cochlear partition is 7 mm. Even so, the volume elasticity does not diminish further at the end of the cochlear partition, and variations of resonance extend only to the 6.5-mm position. The lowest frequency at this point is 400 cps.

The Rat. In the mouse the cochlear dimensions, especially for the diameter of the canal, are too small for reliable measurements. Therefore, as a basis for further study, the rat's cochlea was investigated.

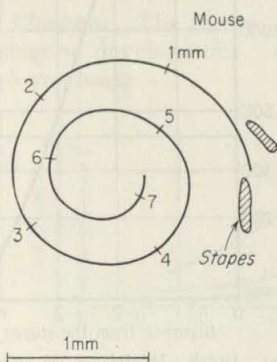


FIG. 12-27. Spiral diagram of the cochlear partition of the mouse.

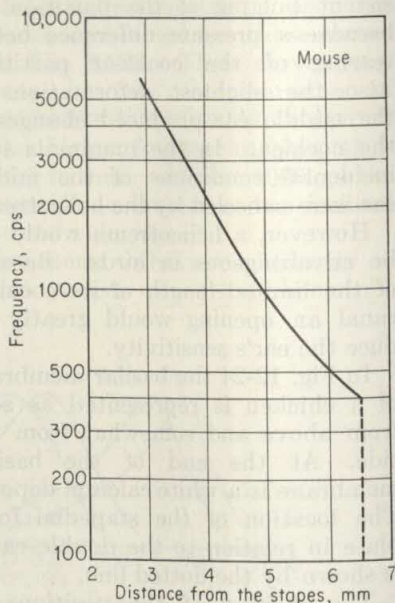


FIG. 12-28. Positions of maximum stimulation along the cochlear partition of the mouse.

The size of its cochlea made it possible to carry out the dissection without particular difficulty. As Fig. 12-29 shows, the length of its cochlear partition is 9.7 mm. The lowest frequency of mechanical analysis is 200 cps, as indicated in Fig. 12-30. Here also the stiffness of the cochlear

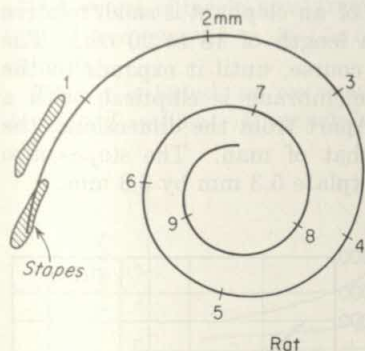


FIG. 12-29. Spiral diagram of the cochlear partition of the rat.

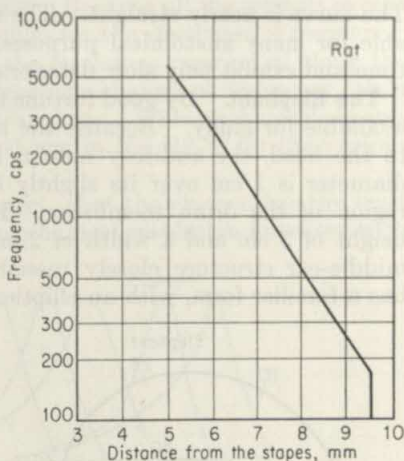


FIG. 12-30. Positions of maximum stimulation along the cochlear partition of the rat.

partition increases from the 9.5- to the 9.7-mm positions, so that resonance extends only to the 9.5-mm point.

The Cow. To determine how the hearing of animals changes with their body size, the cochlea of the cow was studied, for it is one of the largest animals readily available. As the diagram of Fig. 12-31 shows, the cochlear dimensions also are great. The total length of the cochlear partition is over 38 mm, and there are $3\frac{1}{2}$ turns. Mechanical frequency analysis extends to 50 cps. The distribution of resonance positions along the cochlear partition for different frequencies may be seen in Fig. 12-32.

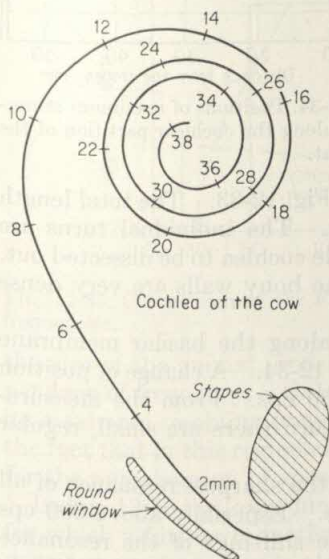


FIG. 12-31. Spiral diagram of the cochlear partition of the cow.

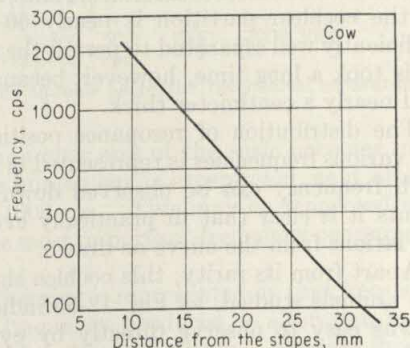


FIG. 12-32. Positions of maximum stimulation along the cochlear partition of the cow.

The curve is nearly straight. The cochleas of cows and calves are suitable for many anatomical purposes, because they stay fresh for a long time and exhibit only slow deterioration of their elastic properties.

The Elephant. By good fortune the head of an adult elephant became available for study. Because the brain of an elephant is small relative to the head, the auditory meatus has a length of 18 to 20 cm. The diameter is 1 cm over its slightly bent course, until it expands in the region of the drum membrane. This membrane is elliptical, with a height of 3 cm and a width of 2 cm. Apart from the dimensions, the middle-ear structure closely resembles that of man. The stapes also has a familiar form, with an elliptical footplate 5.3 mm by 3.8 mm.

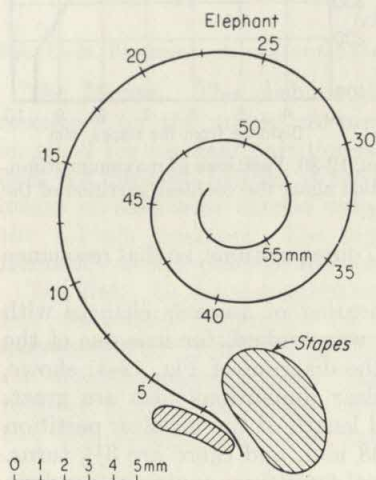


FIG. 12-33. Spiral diagram of the cochlear partition of the elephant.

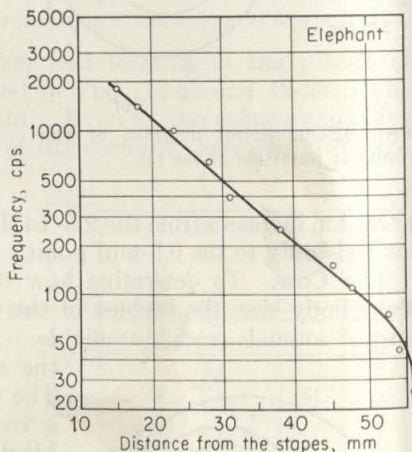


FIG. 12-34. Positions of maximum stimulation along the cochlear partition of the elephant.

The cochlear measurements are shown in Fig. 12-33. The total length of the cochlear partition is nearly 60 mm. The individual turns are sufficiently well separated to permit the whole cochlea to be dissected out. This took a long time, however, because the bony walls are very dense and nearly a centimeter thick.

The distribution of resonance positions along the basilar membrane for various frequencies is represented in Fig. 12-34. A change of position with frequency can be observed down to 30 cps. From the measurements it is clear that in practically every turn there are small, regular deviations from the curve as drawn.

Apart from its rarity, this cochlea shows the sharpest resonance of all the animals studied, as Fig. 12-35 indicates. Especially above 500 cps it was easy to observe directly by eye the shiftings of the resonance points as the frequency was altered, because when the amplitude was suitably adjusted the cochlear position was seen to vibrate over only a few millimeters. At 1000 cps the logarithmic decrement was $\delta = 0.9$.

Comparison of the Different Animals. Because all the animals except the elephant gave nearly the same values for the sharpness of resonance, it is possible to take the shifting of the resonance position Δl along the cochlear partition for a certain percentage change of frequency $\Delta n/n$ as a measure of mechanical frequency analysis. This mechanical separation of frequency $A = \Delta l/(\Delta n/n)$ is shown in Fig. 12-36 for the various animals.

Here it is found, as we would expect, that the chicken has the least developed cochlea. In general the mechanical resolution increases with

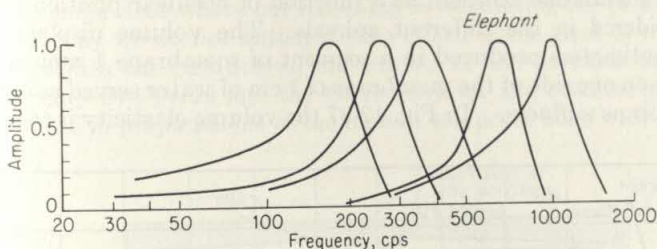


FIG. 12-35. Resonance curves for the cochlear partition of the elephant, at five positions.

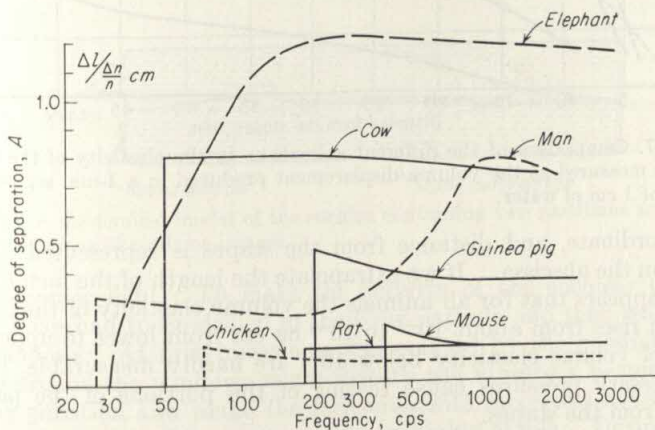


FIG. 12-36. Comparison of the different animals as to the mechanical separation of frequencies.

the size of the animal, and at the upper end of the scale becomes independent of frequency. Only the human ear is exceptional, as it attains its maximum resolving power at 1000 cps. This may be connected with the fact that in this region are the most important frequency components for the apprehension of speech.

In Fig. 12-36 the lower limit of hearing is represented by that frequency for which a further reduction in frequency produces no alteration in the distribution of amplitude along the cochlear partition. Because there is often a moderate increase in the stiffness of the cochlear partition in the neighborhood of the helicotrema, the resonance positions do not continue

their displacements to the extreme end of the partition. Therefore the effective length of the partition is smaller than the actual length.

As is evident in Fig. 12-36, the lower limit of hearing falls as the size of the animal increases. This fact perhaps may be connected with the general enlargement of the ear. When sound is spread along the main surfaces its absorption is less for low frequencies than for high frequencies when the passages are broad, and therefore there is a favoring of the low tones.

Elasticity of the Cochlear Partition for Various Animals. The variation of membrane stiffness as a function of cochlear position is still to be considered in the different animals. The volume displacement in cubic centimeters produced in a segment of membrane 1 mm long by a pressure on one side of the membrane of 1 cm of water served as a measure of membrane stiffness. In Fig. 12-37 the volume elasticity is represented

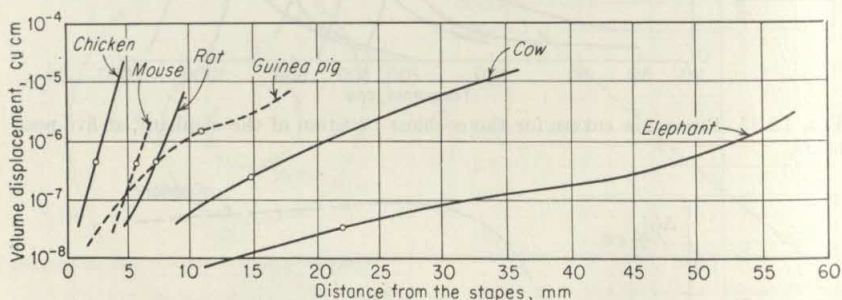


FIG. 12-37. Comparison of the different animals as to the elasticity of the cochlear partition, measured as the volume displacement produced in a 1-mm segment by a pressure of 1 cm of water.

on the ordinate, and distance from the stapes is represented in millimeters on the abscissa. If we extrapolate the length of the membrane to zero, it appears that for all animals the volume elasticity of the cochlear partition rises from about 10^{-9} to 10^{-5} cu cm from lower to upper ends. Values of volume elasticity below 10^{-8} are hardly measurable, because the necessary pressures cause tearing of the portions of the partition distant from the stapes.

For a better comparison of the various animals, a circle has been added to each curve of Fig. 12-37 to indicate the volume elasticity obtaining at the resonance position for 1000 cps. This value is constant only for the very small animals, for which it is 4.5×10^{-7} cu cm.

PARADOXICAL WAVE TRAVEL ALONG THE COCHLEAR PARTITION*

In the inner ear there is a paradoxical vibration of the cochlear partition. This is an unfortunate situation. But analysis of the movements inside the cochlea presents in part a problem in hydromechanics, a field in which plausible reasoning has commonly led to incorrect results.

* Article 73 as listed in the Author's Bibliography. Published in 1955.

Birkhoff has collected enough of these physical paradoxes to make a fair-sized book. The paradox of hydrostatic pressure is probably the best known. The fact that the pressure of a fluid at rest under gravity on the base of a vessel is independent of the size and shape of the vessel is not simple to explain. It is said that in the seventeenth century Pascal demonstrated its validity to the king of France by attaching a small tube to a barrel filled with water. A glass of water poured into the tube was enough to increase the pressure inside the barrel so much that it burst. I do not think that this demonstration would satisfy everybody today; it does not make clear where our reasoning in estimating the pressure was wrong, and why we do not anticipate the effect of the glass of water.

In the cochlea the paradoxical movements of the partition are easily seen. Twenty-five years ago the movements of the cochlear partition were observed in preparations of the human temporal bone with the help

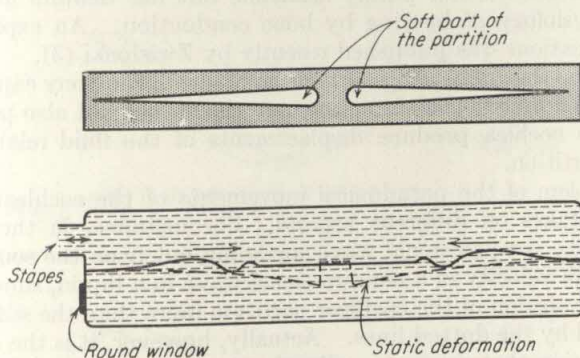


FIG. 12-38. A mechanical model of the cochlea containing two partitions arranged in contrary positions like mirror images.

of stroboscopic light. To make the activity of the cochlear partition visible, holes had to be drilled in the bony capsule and then sealed with glass windows. At first uneasiness was created by the possibility that leakage around the windows might disturb the vibratory pattern of the cochlear partition and make the measurements incorrect; however, the pattern measured in this way proved to be highly stable. During stimulation with a continuous sinusoidal tone, traveling waves moved toward the helicotrema independently of the location and tightness of the windows. To obtain better control of the experimental conditions, a model of the cochlea was made having the same vibratory pattern as the normal ear, but with two cochlear partitions, one facing the other like a mirror image, as shown in Fig. 12-38. In one of the partitions the yielding portion was far from the stapes, as in the normal ear, but in the other the yielding portion was close to the stapes. When the stapes was set in vibration, waves traveled toward the yielding portion in each membrane. In the normal membrane the waves traveled away from the stapes, that is, away from the vibrating source, but in the other membrane they traveled toward the vibrating source.

In general we assume that every vibrating body produces, in a medium, waves that travel away from the source. A wave that travels toward the source may therefore be considered a paradoxical phenomenon. Later experiments showed that even in small cutout sections of cochlear partitions the direction of the waves is independent of the location of the vibrating source.

The problem of traveling waves has been discussed by Tasaki, Davis, and Legoux and by Wever and Lawrence (1), who used the microphonics as indicators of the movement of the cochlear partition (see also Wever, Lawrence, and Békésy).

In normal situations in anatomy the yielding portion of the cochlear partition is far from the stapes, and the waves travel away from the stapes. The question of what happens in the cochlea when the stapes is removed from its usual location and placed at the opposite end of the cochlear partition is not purely academic but has definite implications for the physiology of hearing by bone conduction. An exploration of these implications was published recently by Zwislocki (3).

We assume that in hearing by bone conduction the bony capsule of the cochlea is deformed; therefore, not only the stapes but also parts of the wall of the cochlea produce displacements of the fluid relative to the cochlear partition.

The problem of the paradoxical movements of the cochlear partition sometimes takes on different aspects. For instance, in the model of Fig. 12-38 the compressional wave spreading out from the sound source, with the high velocity of a compressional wave in a liquid, should deform the yielding portion of the cochlear partition more than the stiff portions, as indicated by the dotted lines. Actually, however, it is the stiffer part of the partition that seems to make the larger excursion and that starts a traveling wave in the more yielding part. In a review article, Licklider discussed the various points of view on this problem. Zwislocki (3), in the paper on wave motion cited above, discussed the application of Hamilton's principle to this phenomenon.

The present section describes a step-by-step exploration by experiments on the formation of traveling waves in a model having properties mechanically analogous to the cochlear partition.

Direction of Travel of Continuous Sinusoidal Waves in a Transmission Line. In daily life, periodic disturbances produce waves that travel away from the vibrating source, as, for instance, the waves on a water surface or along a rope. The writer cannot recall having seen in nature a wave traveling toward the source. The first such wave to be observed was the movement along the cochlear partition in a human ear. For this reason such mechanical movement seems paradoxical.

In the study of electrical transmission lines, however, the situation is altogether different. There it is known that in a ladder-type high-pass filter the phase of the continuous sinusoidal output voltage of each section is advanced relative to the input voltage of the same section. Figure 12-39*b* shows a ladder type of high-pass filter with the generator voltage located on the left. With each increase in the number of sections from

the generator along the transmission line there is an advance in the phase of the voltage across the filter relative to the input voltage. If we assume that each section advances the phase 30° , with the help of the familiar scheme in Fig. 12-39a we obtain the voltage pattern along the transmission line at a given instant, as indicated by the solid line in Fig. 12-39b. If we

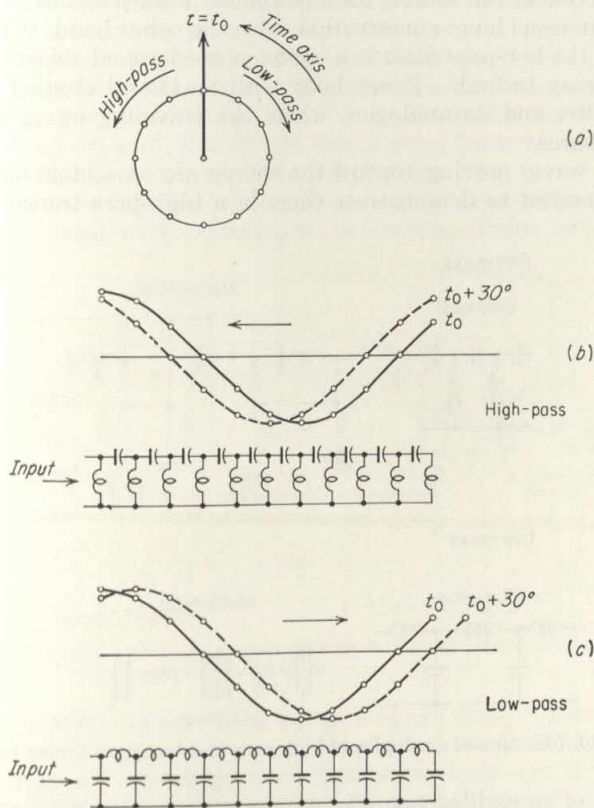


FIG. 12-39. Patterns of voltage waves in transmission lines. (a) is a schema for determining the voltage pattern at any instant. (b) represents an iterative high-pass filter, with the solid curve giving the voltage pattern at a given instant and the broken curve this pattern after the time axis has rotated 30° . (c) represents similarly a low-pass filter.

wait until the time axis has rotated 30° and repeat the procedure, the voltage pattern along the transmission line will be represented by the broken sinusoidal curve. When we compare the solid line with the broken line, we see that the electrical wave pattern along the transmission line moves toward the voltage source. The same procedure applied to a low-pass filter, however, yields a wave pattern moving away from the source, as seen in Fig. 12-39c. Thus we see that in electrical transmission lines there are spatial wave patterns that move either toward or away from the source.

Since every electrical system has an analogous mechanical system, it should be possible to produce spatial wave patterns of both kinds mechanically. In Fig. 12-40 the rectilinear analogy of high-pass filters and low-pass filters is reproduced according to Olson. It is not surprising that in rectilinear movement in general we do not see waves that travel in the direction of the source, for a rectilinear high-pass filter is a complicated and unusual lever construction. On the other hand, the rectilinear analogy of the low-pass filter is a common mechanical structure, easy to build and easy to find. Every body with mass and elasticity acts as a low-pass filter and its analogies, where the traveling waves move away from the source.

Because waves moving toward the source are so seldom encountered, it was of interest to demonstrate them in a high-pass transmission line.

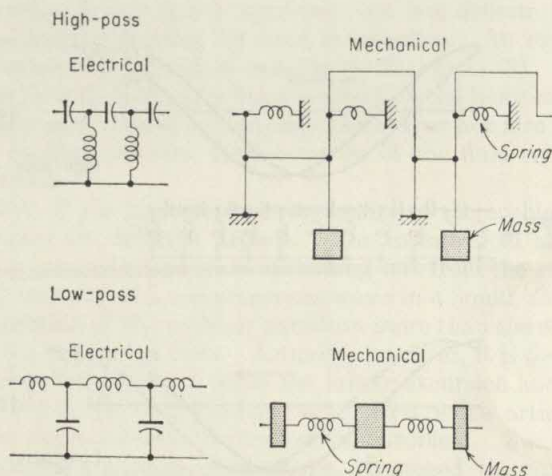


Fig. 12-40. Mechanical analogies of high-pass and low-pass transmission lines.

The y axis of an oscilloscope was connected by a moving contact to one section after another of the filter (Fig. 12-41), and at the same time the spot of the oscilloscope was displaced along the x axis in linear steps with a second contact moving along a potentiometer. In general, as was found in Fig. 12-39, ten discrete dots were enough to show the direction of the displacements of the electric voltage wave along the transmission line. The frequency of the input voltage was $\frac{1}{4}$ cps; $10\text{-}\mu\text{f}$ condensers were used. In place of expensive inductors, $100,000\text{-ohm}$ resistors were used. A potentiometer adjustment made all the excursions equal on the y axis. The rotating contacts swept along the whole transmission line ten times per second to make the spot of the oscilloscope free of flicker.

Mechanical Model with Traveling Waves Analogous to Those Observed in the Cochlear Partition. At first glance the cochlear partition appears to behave under stimulation like a transmission line. But from the electromechanical analogies it is apparent that it is not simply a high-

pass transmission line; we must look for other ways of explaining why the waves travel toward the vibrating source.

The cochlear partition closely resembles a ladder type of transmission line with driving forces that are not exerted on the first section alone but on every individual section. This corresponds to the situation represented in Fig. 12-38, where the fluid pressure produced by a displacement of the stapes spreads out over the whole area of the cochlear partition. The magnitude of the driving force is not uniform along the whole partition; in general, the forces are greatest near the pressure source. Our problem, therefore, is to explain how it is possible that the waves in the cochlear partition do not always travel away from the point of maximum driving pressure but may travel toward it.

To facilitate the experiments it seemed desirable to find an analogous mechanical system with traveling waves having similar properties. It

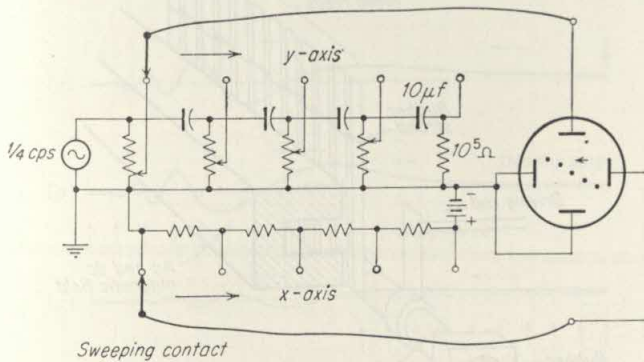


FIG. 12-41. Method of observing the movements of voltage waves in a high-pass transmission line.

was found that a system made up of a single line of tuned resonant reeds, as in a Frahm frequency meter, with each reed coupled to its neighbor, produced traveling waves similar to those seen in the cochlea of a living guinea pig. Each reed was a flat steel spring with a small mass on its top; the size of the mass was varied to adjust the tuning of the reeds. The lower ends of the reeds were attached to a longitudinal vibrating support (Fig. 12-42) with both ends mounted on rubber springs in such a way that the support was able to rotate on its axis without lateral movement. The support could be clamped to a heavy metal block when the design of an experiment called for a fixed support.

There were three ways of setting the reeds in vibration. First, if the driving force was to be applied to a single reed, a rod driven by an electrodynamic system was clamped to the reed. Second, if the force was to be applied with equal strength to all the reeds, the same driving rod was attached to a lever connected to the vibrating support (Fig. 12-42). And third, if the driving force was to be applied to a given smaller or larger section of the reeds, an electromagnetic system was employed. It consisted of an iron core, magnetized with direct and

alternating current, with a slit close to the steel spring of the reed. When the electromagnet was used, the vibrating support was clamped to the metal block to minimize interaction between the reeds.

Two different types of coupling between the neighboring reeds were used: elastic coupling and combined mass-and-friction coupling. Elastic coupling was obtained by winding a single soft rubber strand with a diameter of about 1 mm in and out between the reeds, as shown in Fig. 12-42. Combined mass-and-friction coupling was obtained by partially immersing the whole row of reeds in water or in oils of various viscosities. The degree of coupling was varied by changing the height of the rubber strand or the height of the surface of the fluid above the footpoint of the reeds.

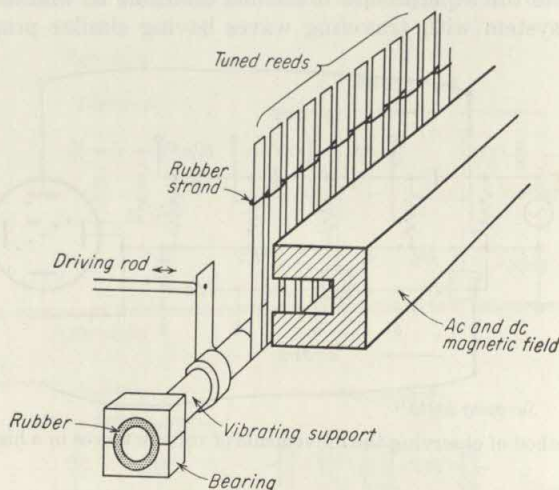


FIG. 12-42. Arrangement of reeds to demonstrate traveling waves.

This model has the properties of the cochlear partition with respect to the direction of the travel of the waves. If the height of the rubber strand decreases continuously from one end to the other, traveling waves appear which move from the stiffest part of the system, at the highest position of the rubber strand, to the more flexible part. This is, to a large degree, independent of the distribution of the driving forces along the reeds. As in the cochlear partition, the wavelength is greatest along the stiff parts of the system and decreases more and more as the waves approach the more elastic parts, until they are completely absorbed. To illustrate this behavior a drawing was made under stroboscopic illumination of the white tips of the continuously vibrating reeds. The pattern of displacement of the tips may be seen in Fig. 12-43*a* to *d*. Figure 12-43*a* shows the displacement pattern when the driving force was acting on only one reed, which here was the reed at the end of the stiffer section. In Fig. 12-43*b* the force was applied to the more flexible section, in Fig. 12-43*c* to the stiff section, and in Fig. 12-43*d* the driving

force was distributed equally along all the reeds. As we see, the differences between the four patterns is small, and the waves may travel toward the driving forces.

In Fig. 12-43*b* there is a small wave traveling toward the stiff part, which is reflected near the stapes and produces a standing wave near the stapes. Its amplitude, however, is small compared to the amplitude of the waves traveling toward the driving force. The four vibratory patterns are even more similar when the height of the rubber strand coupling the reeds starts to decrease immediately near the stapes, corresponding to the situation in the basilar membrane. In this case the

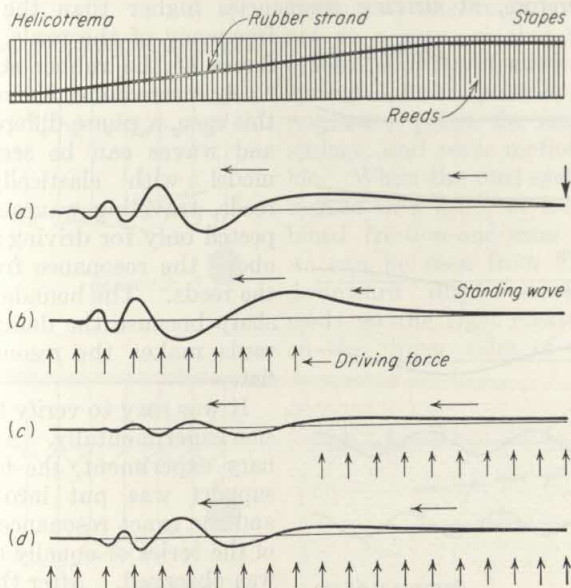


FIG. 12-43. The upper drawing shows how the rubber band was interlaced among the reeds to give coupling that produced traveling waves like those of the cochlea. The waves shown below represent different ways of actuating the system. In (a) vibrations were applied to one reed on the right, in (b) to the more flexible half of the reeds on the left, in (c) to the stiffer half of the reeds on the right, and in (d) to the support.

section with the standing wave is so short that the wave can hardly be recognized. To make it more easily visible, a section with constant coupling was introduced near the stapes.

The next step was to investigate the dynamic properties of this model and to try to account for the paradoxical direction of traveling.

Conditions Necessary for the Formation of Traveling Waves in the Model. A sinusoidal force applied to the model described does not necessarily produce traveling waves. Sometimes a whole section of reeds is simultaneously displaced near the place at which the force is applied, but no waves can be seen. The main characteristic of a wave is a difference in phase between the movements of neighboring parts of a system. A number of conditions must be fulfilled before a phase differ-

ence can be produced. For instance, let us examine two neighboring reeds connected by a rubber strand as shown in Fig. 12-42. The reeds are kept in their zero position by elastic forces, and if a neighboring reed is displaced, the rubber strand will pull on the observed reed. With slow displacements all the forces acting on the reed are purely elastic. There is no important difference between the static deformation pattern along the reeds and the pattern produced by slow oscillations. In both cases all the displacements occur simultaneously, and no waves can be seen.

As the driving frequency is increased, the reeds lose their purely elastic behavior; and above the resonant frequency the reeds act like a mass. Therefore, at driving frequencies higher than the resonance

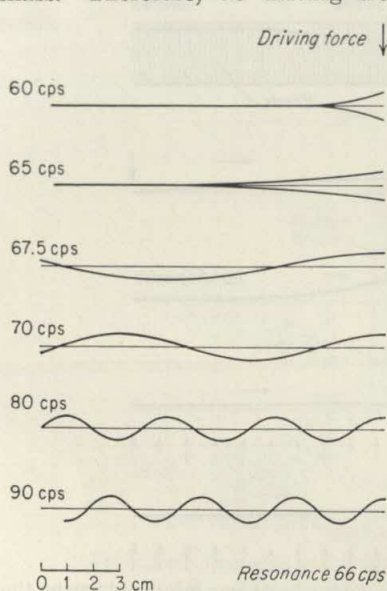


FIG. 12-44. Effects of driving the reed system at frequencies above and below the common resonant frequency of 66 cps.

frequency of the reeds, the elastic forces of the rubber strand effectively interconnect the masses. In this case, a phase difference occurs and waves can be seen. In the model with elastically coupled reeds, traveling waves can be expected only for driving frequencies above the resonance frequency of the reeds. The boundaries are not sharp because the damping of the reeds makes the resonance curve flat.

It was easy to verify this conclusion experimentally. As a preliminary experiment, the longitudinal support was put into vibration, and the exact resonance frequency of the series of equally tuned reeds was observed. After this, the single rubber strand was inserted between the reeds, and the resonance frequency again was determined. For a resonance frequency of 65

cps the change was less than 0.1 cps. This proved that the rubber strand had a negligible mass, and when it was used as a coupler between the reeds only its elasticity played an active part.

To test this conclusion, the driving rod in Fig. 12-42 was attached to the extreme left side of the series of equally tuned reeds, and the momentary pattern of vibration was observed stroboscopically for various frequencies. The sketches in Fig. 12-44 offer experimental proof of the conclusion that traveling waves occur only when the frequency of the driving force is higher than the resonance frequency of the reeds. It should be pointed out how much more quickly the wavelength decreases with increasing frequency in the reed system than in a homogeneous medium. If the driving force has exactly the frequency of resonance of the reeds, the wavelength is infinitely long.

A simple demonstration set up for the same purpose can be seen in Fig. 12-45. It consists of a series of pendulums of equal length coupled by small masses hanging between them. In this special case gravity acts as an elastic restoring force for the mass of the pendulum and the coupling. The swing of the heavy pendulum on the right was used as a generator, and no waves were produced when the generator pendulum was longer than the other coupled pendulums.

If we now leave elastic coupling and investigate mass coupling, we expect a different situation. In mass coupling there should be no traveling waves for driving forces above the resonance frequency,

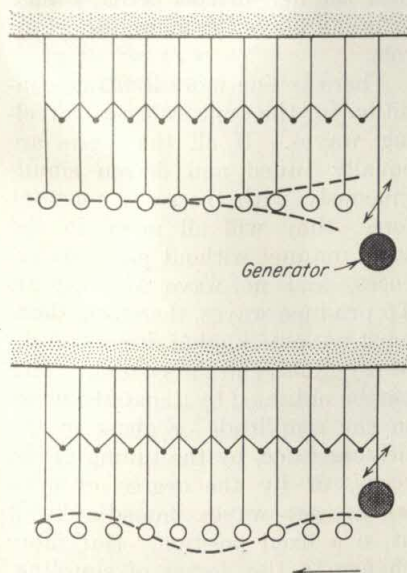


FIG. 12-45. A pendulum model to demonstrate the effects shown in Fig. 12-44.

because at this frequency the reeds act as a mass so that the whole system consists of masses without springs. At frequencies below the resonance point the reeds act as springs, and wave motion is possible. When the reed system is immersed in a fluid, we have a combined friction-and-mass coupling. As can be seen from Fig. 12-46, downward displacement of the reeds on the right creates suction on the upper sides of the reeds

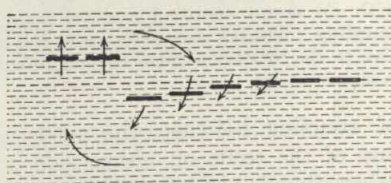


FIG. 12-46. Interaction of the reeds immersed in water as a result of mass coupling.

and pushes the neighboring reeds upward. With elastic coupling the neighboring reeds would move in the same direction as the driving reeds. This reversal in the direction of the coupling forces changes the traveling pattern so that now waves are produced for driving frequencies below the resonance point of the reeds. The direction of the wave travel, however, is not changed. It is in both cases away from the vibrating source, as the experiment demonstrates, because in both cases we have the same type of alternating series of springs and masses. In one case, the spring represents the coupling; in the other, the spring represents the reed.

The sketch in Fig. 12-47a may serve to summarize what happens to a series of reeds whose resonance frequency continuously decreases from left to right. The relative position of the driving frequency is indicated

by the broken line. Figure 12-47*b* sketches the expected wave pattern for elastic coupling with all the displacements in phase between the stapes and the resonant reed. Figure 12-47*c* sketches the expected wave pattern for mass coupling; the wavelength decreases from the stapes to near the

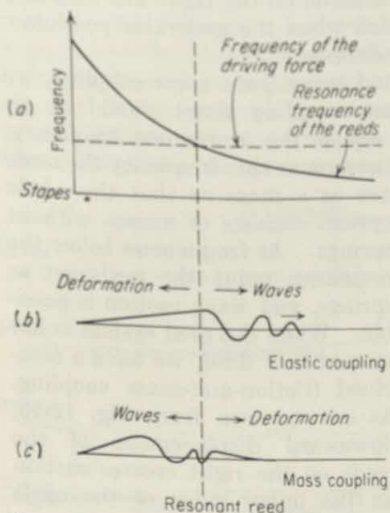


FIG. 12-47. Traveling waves in systems with (b) elastic coupling and (c) mass coupling. The resonance frequency relative to the frequency of the driving force is shown in (a).

of coupling between the reeds. We can get waves immediately if one of the reeds on either side is put in a fixed position. But more interesting is the effectiveness of a change in the degree of coupling. When a constant driving force was applied to the whole series of reeds, traveling waves were obtained with large amplitudes when the height of the rubber strand (Fig. 12-42) was given a discontinuity or was decreased continuously. The last case produced especially beautiful traveling waves similar to those found in the cochlea, so that we expect that there too the continuous change in coupling from the stapes to the helicotrema may play a role in the production of the waves.

When the resonance frequency of the reeds and the driving force were constant along the whole series, a sudden change in the degree of the coupling produced waves whose amplitudes increased with the size of the change in coupling (Fig. 12-48). The waves traveled in both directions from the place of the discontinuity of the coupling, as if the driving force were acting not equally on all the reeds, but only on a single one at the locus of the discontinuity.

Formation of the Paradoxical Direction of Traveling Waves. Two sets of tuned reeds were made in order to investigate the paradoxical waves. One was made with constant tuning and the other with con-

resonant reed, but from there to the helicotrema no waves can be seen.

The actual cochlea is a combination of both kinds of coupling. Near the stapes elastic coupling seems to predominate, whereas near the helicotrema perhaps mass coupling plays the more important role.

There is one more limiting condition for the appearance of traveling waves. If all the reeds are equally tuned and driven simultaneously with the same constant force, they will all move in the same manner without phase differences, and no wave will appear. To produce waves, therefore, there must be some kind of discontinuity or asymmetry in the system. This can be obtained by a spatial change in the amplitude or phase of the driving force, by the tuning of the reeds, or by the degree or type

tinuously decreasing resonant frequencies. In both sets the coupling produced by a rubber strand above the footpoint of the reeds was decreased. By appropriate adjustment of the slope of the rubber strand, traveling waves with an amplitude and phase distribution similar to those in the human cochlea were obtained in both models (page 462). The following experiments were performed on these two models.

First, it must be pointed out that when the driving force was applied to a single reed only, either on the more flexible side (corresponding to the part of the cochlear partition near the helicotrema) or on the stiff side (corresponding to the part near the stapes), there was no paradoxical wave. The waves always traveled away from the driving source. However, when the driving force was applied to a greater length of the reed system, the paradox was usually apparent.

In both the model and the living cochlea it seems that the stiffer part of the system drives the more yielding part. This view is corroborated

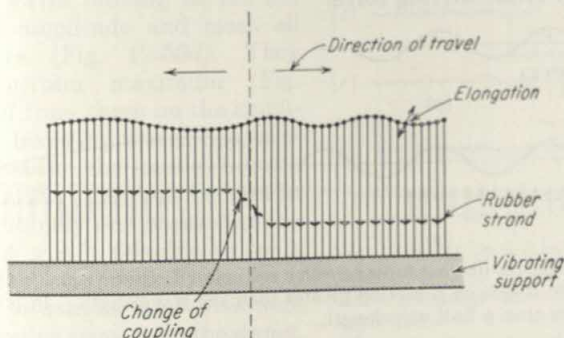


FIG. 12-48. Traveling waves produced by a change of coupling.

by the fact that pressing damping material against the vibrating stiffer parts also immediately decreased the amplitude of the waves in the more flexible parts. But, when the damping material was applied to the more flexible parts of the system, the effect on the stiff parts was small. This argument holds true even for smaller sections of the partition. However, it must be pointed out that along a small section of the system the damping of the traveling waves is slight, and for this reason, at certain frequencies, the reflection of the waves from both ends of the section will produce standing waves. In some frequency ranges these standing waves may distort the amplitudes along the section.

Our problem is to determine why it is that, with a broad distribution of the driving forces along the system, it is primarily the stiffer parts of the system that are set in motion, so that the waves move from there to the more elastic parts. As far as the writer can see, three effects combine to produce this phenomenon: (1) there is a cancellation of the driving force for the section of the system with short waves; (2) the wavelength along the system decreases rapidly; (3) as waves travel from the stiff parts to the more elastic parts the amplitude of their displacement

increases, much as the movements of air particles in a loudspeaker horn become greater as the diameter of the horn is increased.

The cancellation effect of the driving force is summarized in Fig. 12-49, which shows the wave at a given instant. As can be seen from drawing *a*, the amplitude of the wave is reinforced as long as (1) the force is at an appropriate position with respect to the wave, and (2) the section upon which the force acts is smaller than or equal to half the wavelength. With a further increase in the length of the section driven, the total reinforcement starts to decrease, and becomes zero when the length of the section upon which the force acts is equal to the wavelength. A still further increase in the length of the driven section will make the reinforcement go alternately through a maximum and through a minimum, as can be seen in drawing *b*, where large sections of the driving forces are canceled out. When the wavelength is greater than the linear extent of the system to which the force is applied, as in *c*, there is no cancellation of the driving force.

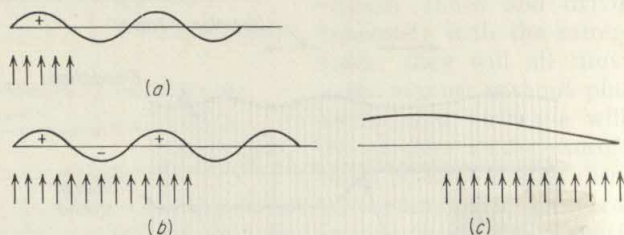


FIG. 12-49. In (*a*) the driving force acts on a section of the wave equal to the half wavelength. In (*b*) it acts on a section greater than the wavelength. In (*c*) it acts on a section smaller than a half wavelength.

The paradox of the direction of the traveling wave results largely from the fact that in a system like the series of reeds, coupled elastically or by masses and friction, and in a system like the cochlear partition, the wavelength drops quickly from a given value to a very small value, so that the situation represented in Fig. 12-49*b* is immediately adjacent to that of Fig. 12-49*c*. When this occurs, the section at one end of the system is completely under the control of the driving forces, whereas the other section is free in spite of the large driving forces, because these cancel each other out.

It is probable that in all systems where for a certain frequency there is a rapid change in the wavelength during travel, the paradoxical direction of travel may be expected. In our system of coupled reeds, as can be seen from Fig. 12-44, the wavelength is infinitely long for 66 cps and drops to 18 cm at 67.5 cps; this change occurs for a change in frequency of 2 per cent. A further change of 20 per cent will reduce the length to one-fourth. In the cochlea of a living guinea pig and in preparations of the human temporal bone, the changes in wavelength are similar. It seems reasonable, therefore, to assume that the section near the stapes receives the energy from the driving force and transmits it to the more yielding parts of the partition.

To show how the traveling waves are formed, use was made of a system of equally tuned reeds with a rubber strand increasing continuously in height from one level to another as shown in Fig. 12-50a. The length of the electromagnetic driving unit is represented by a heavy line above each of the drawings of vibratory patterns for various positions of the same driving unit. At the extreme left, the whole driving unit is in a section where the height of the rubber strand is constant. No waves are produced because only a change in the coupling would produce a wave (Fig. 12-50b). When the driving unit is pushed farther to the right, the waves moving to the right increase in amplitude and mask all other waves (Fig. 12-50d). They reach a certain maximum (Fig. 12-50e), and from there on the amplitude of the traveling waves decreases slightly because the reeds become stiffer and stiffer. As can be seen in Fig. 12-50, in only one position of the driving unit was it possible to see a small wave moving toward the stapes; in all other situations the waves were always traveling away from the stapes, toward the more flexible part. During the lateral displacement the electromagnetic driving force exerted on the reeds was kept constant.

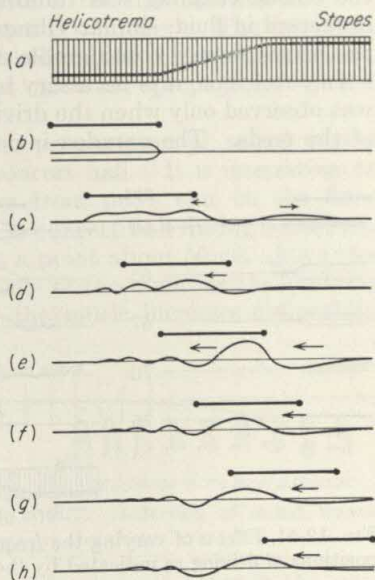


FIG. 12-50. At (a) is shown the form of elastic coupling of the reed system. The remaining drawings show the application of the driving force to different sections as indicated by the heavy lines.

The above-mentioned horn effect, which once more places the emphasis on the waves traveling toward the more flexible parts, can be seen in Fig. 12-50h. Because of the stiffness of the reeds on the right side the amplitude of the traveling waves is small at first but increases as the waves reach the more flexible part of the system, until the wavelength becomes small and the waves are absorbed.

The increase in the amplitude during traveling is a transformation of small movements and large forces near the stapes into large movements and smaller forces near the helicotrema. The energy of the wave remains nearly constant.

To complete the picture of the formation of traveling waves for the same system of reeds, the driving unit was placed at the extreme left, middle, and extreme right, and the vibratory pattern was recorded (Fig. 12-51) while the driving frequency was being increased. When waves could be seen, they were traveling toward the more flexible parts of the reed system.

The same experiments were repeated with a series of reeds that were

weighted on the ends with small lead balls. The resonance frequency of the reeds diminished as the height of the rubber strand decreased. No change was found in the essential behavior of the system. When the elastic coupling was removed and the whole system of reeds was immersed in fluid, similar vibratory patterns were obtained, except that the waves showed considerable damping.

In conclusion, it is necessary to point out that paradoxical wave travel was observed only when the driving forces were applied to a large section of the reeds. The paradox is described only for continuous stimulation

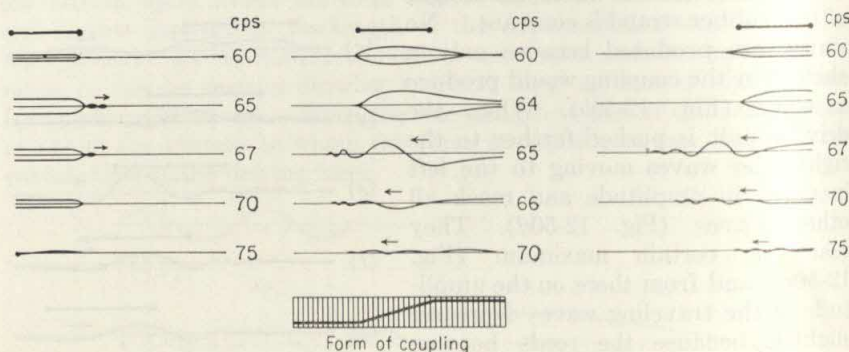


FIG. 12-51. Effects of varying the frequency of the driving force, with three different positions of driving as indicated by the heavy lines at the top.

where the so-called phase velocity of the traveling waves is seen. Waves produced by a sharp click, where so-called group velocity is seen, are not considered.

SIMPLIFIED MODEL TO DEMONSTRATE ENERGY FLOW AND TRAVELING WAVES*

Our concepts of waves have developed mainly from our experience with waves on the surface of fluids and waves of light, where the so-called geometric rules of optics seem to be particularly applicable. Ordinarily the waves we deal with are propagated in or along a homogeneous medium. In the basilar membrane, however, the waves travel along a medium that changes its physical properties continuously. Experiments show that under these conditions the familiar rules of wave propagation may lead to wrong conclusions.

Let us consider, for instance, a well-known demonstration used to show the diffusion between two fluids. As can be seen in Fig. 12-52, a concentrated copper sulfate solution is placed in the bottom of a plane-parallel glass trough, and on top of this a layer of plain water is floated slowly in order to avoid any turbulence. In a short time the copper sulfate diffuses into the water, and the color of the mixture shows a continuous transition. If a small horizontal light beam enters the

* Article 78 as listed in the Author's Bibliography. Published in 1956.

trough close to the bottom, it crosses the trough without any change in its direction of travel. But if the light beam enters the trough at a level at which the diffusion is taking place, then, as Fig. 12-52 shows, the light beam is deflected downward, in spite of the fact that the index of refraction in the horizontal plane is constant (O. Wiener). The deflection increases with the gradient of the vertical change in the refractive index. Thus the simplified geometric concept of wave propagation is not applicable.

A similar phenomenon occurs in the propagation of sound waves above the heads of the audience in a concert hall. It is interesting to rise from one's seat on the floor of a concert hall during a concert. At a point about 50 cm above the heads of the audience the loudness of the music increases noticeably,

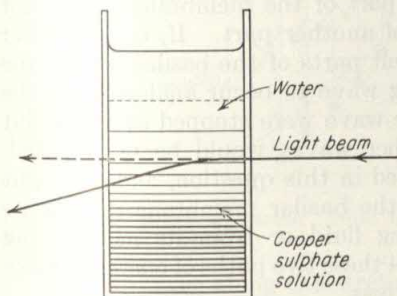


FIG. 12-52. Deflection of a light beam in a region of diffusion.

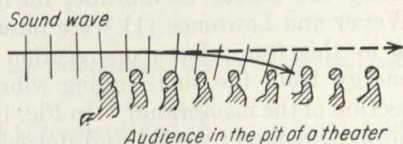


FIG. 12-53. Deflection of sound waves near an absorbent layer.

in spite of the fact that there is no visible obstacle between the performer and the seated listener. It is possible to show experimentally that the mere presence of an absorbing layer parallel to the pathway of the sound decreases the amplitudes of the sound waves (page 395) and deflects them from their straight path of propagation (see Janovsky and Spandöck; and Fig. 12-53).

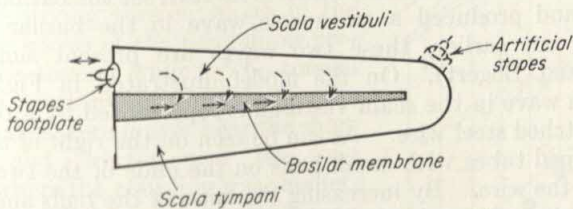


FIG. 12-54. Schematic drawing of the cochlea.

In both these examples the continuous change in the medium is perpendicular to the direction of propagation of the waves. In the cochlea, however, the continuous change takes place along the direction in which the waves travel, and under these circumstances the phenomena are even more complicated. A schematic drawing of the cochlea is presented in Fig. 12-54. The alternating air pressure in the meatus sets the eardrum and then the stapelial footplate into vibration. These vibrations are transmitted to the fluid that surrounds the basilar membrane. Under stroboscopic illumination the traveling waves of the

basilar membrane can be observed in living guinea pigs and in preparations of the human temporal bone (page 441). They can also be calculated.* The question that concerns us here is whether pathological changes in the basilar membrane are likely to cause changes in the traveling waves. For instance, if the part of the basilar membrane close to the stapedial footplate becomes solidified, how will this affect the movements at the other end of the basilar membrane? According to Helmholtz's conception, each section of the basilar membrane moves fairly independently, without strong coupling with its neighbors. Each section is assumed to receive its energy directly from the fluid pressure acting on it, and solidification of one part of the membrane would not have much effect on the movements of another part. If, on the other hand, the coupling between the adjacent parts of the basilar membrane is strong, we should expect a traveling wave to occur analogous to the waves observed on ropes. Then if the wave were stopped at any point along the basilar membrane, no further waves would be propagated. Wever and Lawrence (1) were interested in this question, and they put it in this form: Does one section of the basilar membrane receive its energy from the surrounding vibrating fluid or from its neighboring section of the membrane? In Fig. 12-54 these two paths of energy uptake are represented by solid and dotted arrows.

In order to investigate in detail the ramifications of this problem, a mechanical model was constructed in which the movements were large enough and slow enough to be observed with the naked eye.

Description of the Model. A sudden displacement of the stapedial footplate in the direction of the helicotrema (to the right in Fig. 12-54) produced a compression wave in the vestibular fluid column of the cochlea, and this wave traveled away from the stapes. This driving pressure wave produced a pressure difference between the vestibular and tympanic scalae of the cochlea, which in its turn set the basilar membrane in motion and produced a transverse wave in the basilar membrane. As pointed out earlier, these two waves are present simultaneously (Peterson and Bogert). On the model illustrated in Fig. 12-55, the compression wave in the scala vestibuli is represented by a torsion wave along a stretched steel wire. As can be seen on the right of the drawing, brass T-shaped tubes with small balls on the ends of the two arms were attached to the wire. By increasing the mass of the balls and the length of the arms, it was possible to slow down the speed of the torsion waves until they could be followed with the naked eye. The basilar membrane with its continuously varying stiffness was represented in the model by a set of pendulums continuously graduated in length and suspended from the vertical branch of the T tube. The pendulums could swing completely free, or each could be coupled to its neighbor by means of small balls suspended from threads between the pendulums (see Fig. 12-55). When the coupling balls were close to the masses of the pendulums the coupling was strong, and when they were close to the suspension the coupling was weak.

* See Ranke, Zwislocki, Peterson and Bogert, Bogert, Licklider, Fletcher (6).

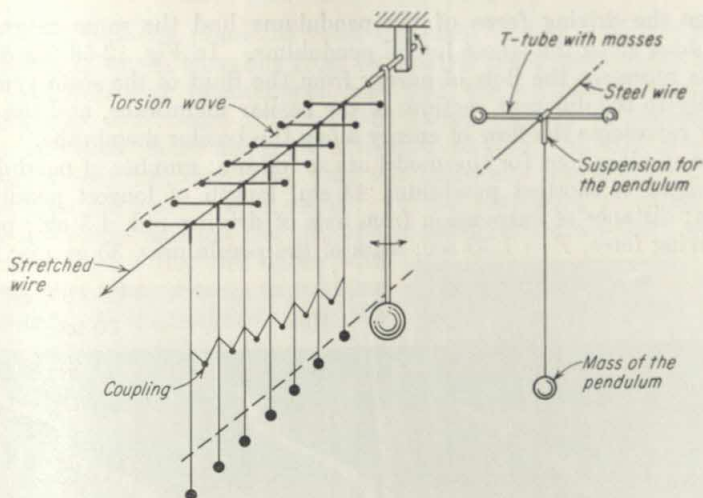


FIG. 12-55. Pendulum model. Note that the pendulums vary in length and are coupled by small balls.

A torsion wave along the stretched wire displaced the suspension and set the pendulums in motion. Increasing the distance between the point of suspension and the axis of the wire increased the driving force acting on the pendulums. Torsion waves were produced in the wire either by a heavy driving pendulum or by an eccentric wheel moved by a synchronous motor at a constant speed.

In this kind of model two waves could be seen, the driving torsion waves of the wire and the waves of the pendulums produced by the torsion wave. The torsion waves had a constant wavelength, but the pendulum waves were longer near the short pendulums and shorter near the long pendulums where the coupling was smaller. Both waves traveled away from the driving pendulum.

In the cochlea itself, the speed of the driving compression waves is much higher than the speed of the waves observed along the basilar membrane. At 1000 cps the ratio in the human cochlea is more than 20:1. Accordingly, the speed of the torsion waves of the model had been made infinitely large by substituting for the stretched wire a solid cylinder oscillating around the axis of the wire (see Fig. 12-56). With this

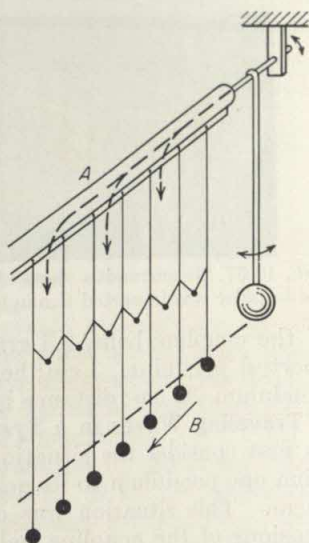


FIG. 12-56. Revised form of the pendulum model. A is a solid cylinder through which the pendulums are driven.

oscillating around the axis of the wire (see Fig. 12-56). With this

change the driving force of the pendulums had the same magnitude and phase along the whole line of pendulums. In Fig. 12-56 the dotted arrows represent the flow of energy from the fluid of the scala tympani directly to the different sections of the basilar membrane, and the solid arrow represents the flow of energy along the basilar membrane.

The specifications for the model are as follows: number of pendulums, 48; length of shortest pendulum, 43 cm; length of longest pendulum, 53 cm; distance of suspension from axis of driving rod, 4.5 cm; period of driving force, $T = 1.35$ sec; mass of the pendulums, 35 grams; mass

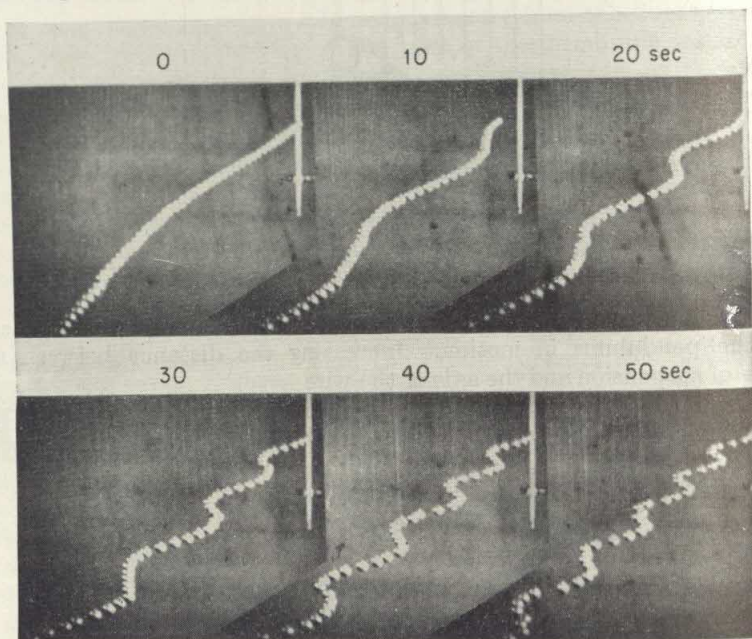


FIG. 12-57. Six successive views of a series of graduated pendulums without coupling. An impulse was imparted through the driving rod on the right.

of the coupling balls, 3.5 grams; height of the coupling balls above the shortest pendulum, 3 cm; height of the coupling balls above the longest pendulum, 35 cm; distance between the pendulums, 5 cm.

Traveling Waves in a System of Pendulums with No Coupling. Let us first consider the situation in which there is no energy transmission from one pendulum to its neighbor because there is no coupling between them. This situation was obtained on the model by raising the suspensions of the coupling balls until they reached the suspension point of the pendulums. The systems then consisted of a series of free pendulums of continuously increasing length.

If the driving axis was suddenly rotated a few degrees, all the pendulums were activated at the same moment, and they began to swing. Since each pendulum had a different period of oscillation, a phase difference soon developed, and the pendulums were no longer in a straight

line. With time this phase difference increased, and an observer had the impression of waves traveling from the shorter pendulums to the longer ones. The striking phenomenon was that the wavelength decreased continuously with time. Figure 12-57 shows a series of photographs taken at 10-sec intervals from a motion picture. Shortly after the pendulums received one push, only one half-wave was seen, but after 50 sec five full-waves were visible. It was surprising to notice that when the waves reached the end of the pendulum series there was no reflection at all. But this agrees with the fact that when there is no coupling no energy is transmitted from one pendulum to its neighbor.

This shortening of the wavelength with time after a sudden push is not observed in the cochlea. Certainly the damping in the cochlea is larger than in the model; nevertheless, when the

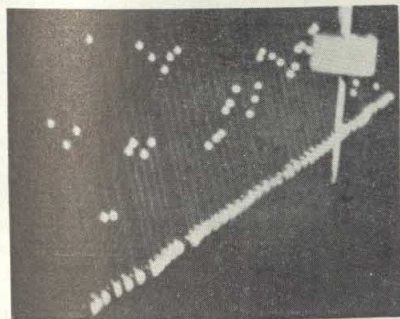


FIG. 12-58. A system containing pendulums of equal length. No waves are formed.

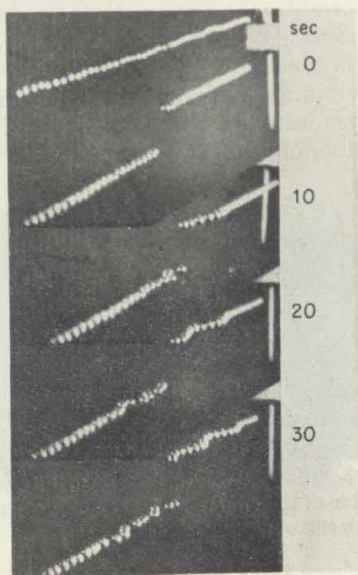


FIG. 12-59. A system containing two lengths of pendulums. Note that waves arise at the place where the change in length occurs.

basilar membrane is plucked, two full periods of vibration can be observed on an oscilloscope that records the aural microphonics (page 644). This would be time enough to observe a decrease in wavelength if there were one. From this we have to conclude that there is an appreciable amount of coupling in the basilar membrane.

Generation of Waves. The waves are produced by the phase difference between adjacent pendulums (Fig. 12-57). If all the pendulums are of the same length, there is no phase difference between them, and, as can be seen in Fig. 12-58, they merely swing back and forth in a line, irrespective of the height of the coupling balls. The waves originate only at the place where there is a change in the length of the pendulums. In order to show this more distinctly, the right-hand half of the pendulums were made a constant short length, and the left-hand half were made a constant longer length (Fig. 12-59). The driving rod began to oscillate at the moment $t = 0$, and, as can be seen from the prints made

from a motion picture, two waves were formed that traveled away from the point of discontinuity, the one traveling to the right with a long wavelength and the other to the left with a much shorter wavelength, mainly because the coupling between the pendulums was less in the left section than in the right section. Both waves showed a well-circumscribed form that traveled with time away from the point of discontinuity.

It is important for an understanding of the different types of wave formation to begin with the conception that wherever a change in stiffness occurs, two waves are formed, one traveling to the left and the other to the right. When there are many changes along the system, they summate and form the final visible wave. When the lengths of the pendulums increase continuously, each section contributes to the formation of traveling waves. The final wave is illustrated in Fig. 12-60,

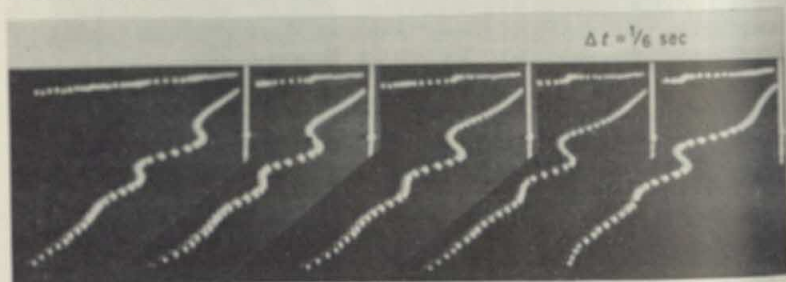


FIG. 12-60. When the length of the pendulums changes progressively there is a summation of the effects of these changes, and a traveling wave forms with a maximum in one place.

where the wave moves from right to left and reaches its maximum amplitude in the middle of the series. These pictures were taken at $\frac{1}{6}$ -sec intervals during steady continuous oscillation. They show a wave pattern similar to that observed in the cochlea. If the frequency of the oscillations was increased, the maximum of the amplitudes moved to the right, thus transforming the frequency change into a displacement of the place of maximal amplitude. Since the pendulum series was relatively short, reflections could not be avoided at both ends of the series, and standing waves could arise.

If we now go back to Fig. 12-59, we can see that every change in the stiffness distributes the energy along the series of pendulums. This distribution takes the form of waves, and therefore the energy may move a long way if the damping of the waves is not too strong.

Energy Transmission to Different Parts of the Membrane. From the previous discussion it is seen that a pendulum receives part of its energy from the oscillating driving rod directly (dotted arrows in Fig. 12-56) and part from its neighboring pendulums (solid arrows). The question therefore is, which part is the larger? In the model the movements of all the longer pendulums could be stopped by pressing against them with a wooden bar covered with foam rubber, as shown in Fig. 12-61.

When this was done, the amplitudes of the movements of the shorter pendulums were not usually diminished but were actually increased, for a standing wave was formed. From this we must conclude that the shorter pendulums received their energy from the oscillating rod and not from the longer pendulums. On the other hand, if the movements of the shorter pendulums were stopped, as in Fig. 12-62, the amplitudes of the longer pendulums were decreased. This can be seen clearly if we compare Fig. 12-62 with Fig. 12-60, which shows the amplitude distribution of the undisturbed waves for the same amplitudes of oscillation of the driving rod. This fact indicates that the flow of energy from the shorter pendulums toward the longer ones is dominant for those pendulums whose amplitude is maximum for a particular driving frequency. An even more convincing experiment was to let the system with the stopped shorter pendulums oscillate until a steady state appeared. Then if the damping foam-rubber board was removed abruptly, the

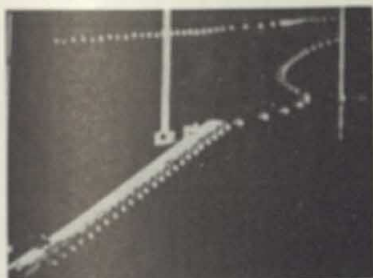


FIG. 12-61. A bar covered with foam rubber was used to stop the vibrations of the longer pendulums.

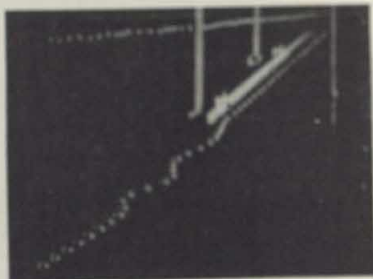


FIG. 12-62. The bar was used to stop the vibrations of the shorter pendulums.

shorter pendulums began to oscillate. When the waves thus formed reached the longer pendulums, they were in opposite phase to the waves formed by the longer pendulums. The result was that the waves canceled one another, and the amplitudes of the longer pendulums were further diminished. It took some time for the phase to become reversed and for the larger amplitude finally to be attained.

The result was similar if one pendulum in the area of maximal amplitude was simply stopped. The amplitudes of the shorter pendulums increased, and those of the longer pendulums decreased.

Still another way to show that the energy of a pendulum tends to flow in the direction of the longer pendulums is to give a small section of the pendulums a push and then to observe the direction of the waves thus produced. The ten longest pendulums were displaced slightly and then suddenly released. As can be seen in Fig. 12-63, the potential energy of this section did not produce a wave of large amplitude traveling toward the shorter pendulums, but, as the picture taken 20 sec after the release shows, the longest pendulum had the largest excursion.

If the damping of the pendulums was increased by letting them swing in water or oil, the energy transmitted from one pendulum to its neighbor

soon diminished. But the general trend was still the same, and when the coupling between the pendulums was increased, the wavelength increased, and with it the distance the energy traveled.

Paradoxical Waves. The tendency of energy to flow from shorter to longer pendulums as a result of coupling leads to some surprising phenomena. In the experiments described above, the length of the driving lever (the distance between the axis of the driving rod and the suspension in Fig. 12-55) was the same for all the pendulums. It was possible, however, to increase the length of the driving lever of the longer pendulums relative to the shorter ones without changing the direction in which the waves traveled. Now the traveling waves moved toward the place where the driving amplitude was higher. This is a startling phenomenon, for we are accustomed to seeing waves move away from the source of sound or vibration. In the experiment illustrated in Fig. 12-64, the same set of pendulums was fixed in an arched curve on the

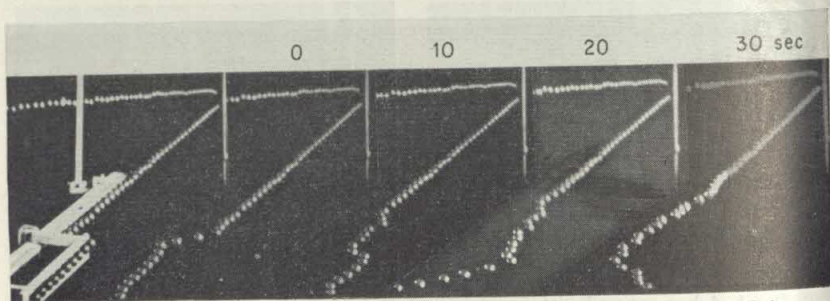


FIG. 12-63. The effects of delivering an impulse to the series of longer pendulums.

oscillating driving rod in such a way that the force acting on the pendulum doubled in size every twelfth pendulum, counting from the shortest one. Since the model contained forty-eight pendulums, the driving force acting on the longest pendulum was sixteen times larger than the driving force acting on the shortest. Although a large amount of energy was transmitted directly from the oscillating suspension to the long pendulums, the waves still traveled in the same direction as before, *i.e.*, from the shorter pendulums to the longer ones, and with a similar pattern and only a slight displacement of the place of maximal amplitude. Anyone watching the waves received the impression that it would take a much greater increase in the driving force to reverse the direction of the traveling waves.

The model represents only a small section of the actual cochlea. Because this unequal distribution of the driving forces did not change the direction of the traveling waves in the model, it is not surprising that in the cochlea, too, the direction of the traveling waves is to a high degree independent of the location of the driving forces. Actually, this phenomenon was first observed on a preparation of the human cochlea (page 425). As shown in Fig. 12-54, substitution for the stapedial footplate of an artificial stapes at the other end of the basilar membrane

(dotted drawing to the right) changed the sensitivity but not the direction of the traveling waves, and beyond this no change was observed under the microscope. Wever and Lawrence (1) recorded microphonics to indicate the vibrations of the basilar membrane and came to the same conclusion. Two mathematical interpretations of the phenomena were presented by Zwislocki (3), one using Hamilton's principle. Some

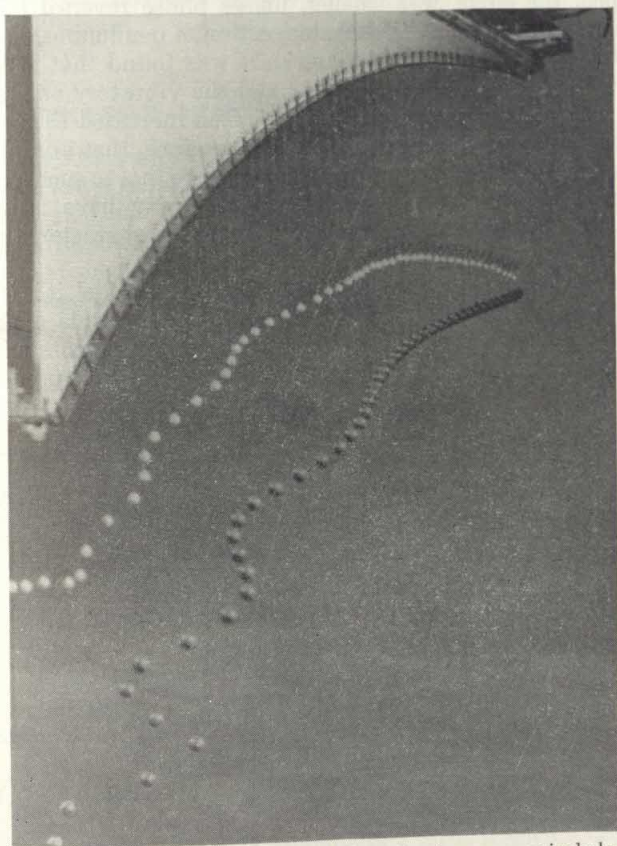


FIG. 12-64. A special arrangement of the pendulums to give progressively larger driving forces to the longer pendulums.

experiments designed to explain this phenomenon were reported above (page 517).

Wave Patterns Corresponding to Pathological Conditions. The pendulum model is especially suited to the investigation of the effect on the general wave pattern of local disturbances such as those found in pathological ears. As Fig. 12-61 shows, stopping a large section of the longer pendulums (analogous to the area near the helicotrema) did not decrease the vibratory amplitude of the shorter pendulums (those near the stapes). But if a section of the shorter pendulums was stopped, as

shown in Fig. 12-62, the amplitude decreased to about one-third of its earlier value. The largest changes in amplitude occurred when a continuous sinusoidal driving force was used and the pendulum with maximal amplitude was stopped. This is shown in Fig. 12-62, where the movement of all the pendulums to the right of the place of maximal amplitude was arrested. If only a small section of pendulums at the extreme right was stopped, the effect was smaller, unless phase reversal produced a cancellation of the waves. If the same section of pendulums was stopped but the driving frequency was changed, it was found that at some frequencies the cancellation was maximal and the vibratory amplitude was minimal. But a small frequency change often increased the amplitudes above their normal value. It is possible, therefore, that abrupt changes in the threshold of hearing with frequency may be due to such a situation. Heretofore, these changes in frequency sensitivity have usually been attributed to abrupt changes in the transmission characteristics of the middle ear.

In order to evaluate the observations made on the model, it is important to remember that an amplitude decrease of 3:1 equals a change in threshold of only 10 db. Clinical threshold measurements are seldom more precise than ± 5 db. This fact limits the safety of speculations.

CHAPTER 13

FREQUENCY ANALYSIS AND THE LAW OF CONTRAST

FREQUENCY ANALYSIS IN THE HUMAN COCHLEA*

Preliminary to the direct determination of the distribution of amplitudes along the cochlear partition, an effort was made to discover the principal assumptions formed on psychological and physiological grounds concerning the distribution of stimuli and excitations. Beatty collected some of the relevant measurements, as shown in Fig. 13-1. There seem to be irreconcilable contradictions between these measurements and the direct observations.

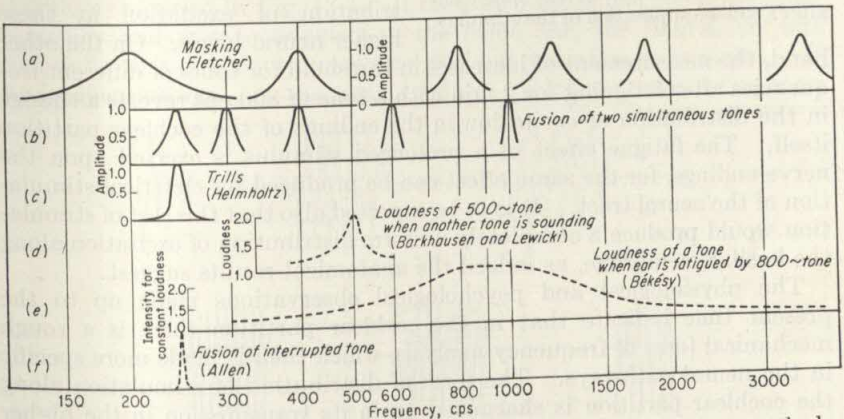


FIG. 13-1. The resolution of frequency by the ear as determined by various methods.

It first must be noted that Helmholtz's measurements of the spread of amplitude along the cochlear partition were based upon the onset and decay of pure tones. He assumed that the onset and decay times of pure tones in the ear were determined solely in a mechanical way, through resonance. This assumption is a most improbable one from a physiological standpoint, for neural processes also have a certain latency and persistence. These relations are best appreciated if the mechanical stimulus is delivered to the surface of the skin rather than to the cochlear partition. In the skin it is possible with care to avoid all resonance phenomena. The latency obtained for the finger tip with a vibration

* A portion of Art. 46 as listed in the Author's Bibliography. Published in 1944.

of 100 cps is shown in Fig. 13-2. The course of this curve shows a general resemblance to that obtained in hearing on the application of pure tones. These latencies may readily be measured by comparing the sensory intensity of a brief vibration or tone pulse with that of a long pulse in which the duration is sufficient to permit the sound to attain its full loudness.

If the other measurements shown in Fig. 13-1 are compared with one another, they fall into two groups. In one group are phenomena that are not affected by the presentation of sounds to the other ear. In the other group are phenomena that remain the same regardless of whether the two interacting sounds are presented to a single ear or are

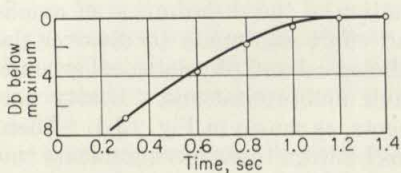


FIG. 13-2. Slow development of vibratory intensity as perceived on the finger tip after a sudden application of the stimulus.

presented separately to the two ears. For this latter group the discrimination of frequencies is particularly good. Because the auditory nerve fibers from the two ears meet only at the higher levels of the nervous system it follows that these measurements reflect the distribution of excitation in these higher neural levels. On the other hand, the measurement of increases in threshold for tones of different frequencies after fatiguing for 2 min with a tone of 800 cps reveals a change in the distribution of excitation in the endings of the cochlear partition itself. The fatigue effect of a prolonged stimulus is exerted upon the nerve endings, for the same effect can be produced by electrical stimulation of the neural tract. It is to be expected also that this sort of stimulation would produce a completely uniform distribution of excitation along the basilar membrane, as indeed the anatomical results suggest.

The physiological and psychological observations made up to the present time indicate that in the cochlear partition there is a rough mechanical form of frequency analysis, which then is made more specific in the neural pathways. The form of distribution of stimulation along the cochlear partition is sharpened up in its transmission in the higher centers, and thus permits a sharper localization. It is not difficult to conceive of further experiments that would prove that a pure tone has a much more extensive representation on the cochlear partition than in the higher neural centers.

The loudness of a pure tone of high intensity gradually falls off in time on account of fatigue. As we have seen, this is a peripheral phenomenon. If beats are produced by means of a second tone of equal intensity, the stimulus magnitude fluctuates continually so that during the silent periods the nerve endings have time to recover. For this reason a beating tone produces hardly any fatigue. This characteristic of nerve endings can be made use of to show how far apart in frequency two tones must be so that their two regions on the cochlear partition will not interact, and they will be heard as distinct tones with no beating. As soon as the spatial separation becomes complete the

usual fatigue effects will again manifest themselves. Figure 13-3 shows that at 2000 cps the frequency separation must be about 500 cps before normal fatigue appears. Again we find a broad area of stimulation on the cochlear partition.

Contrast Effect. If loudness is used instead of fatigue in the attempt to determine the distribution of stimulation, we find that higher nervous centers are involved. Loudness is always affected in some degree by the

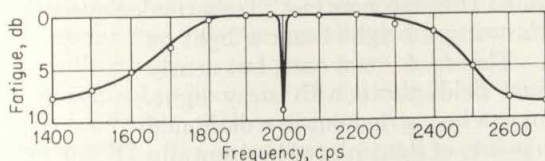


FIG. 13-3. Fatigue effects of two beating tones as a function of frequency separation.

interaction of the two ears, and in this interaction the discrimination of frequencies is enhanced. The following experiment illustrates this point. Two series of tone pulses were presented with envelopes as nearly uniform in amplitude as possible and were alternated with one another as pictured in Fig. 13-4. If these two series had the same tonal frequency and were conducted to the same ear, the impression was essentially that of a continuous tone without variation in loudness. If the frequencies were not the same, loudness variations appeared as soon

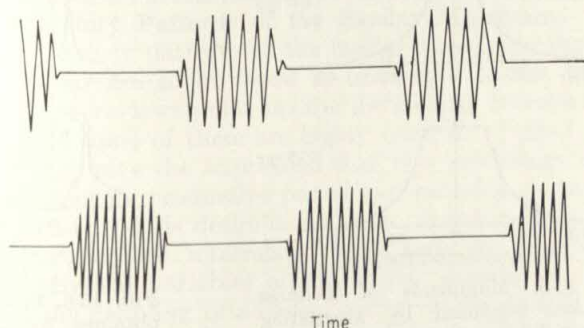


FIG. 13-4. Two series of pulses, with each pulse in a series filling the silent period between pulses in the other series.

as the two tones excited separate portions of the nerve center for loudness. Then the two pulses could no longer be fused, but appeared in consciousness separately. The sizes of the loudness variations were measured for various amounts of frequency separation and are shown in Fig. 13-5. It is clear that at 2000 cps a difference of 60 cps was sufficient to give a complete separation of the two pulses. Because there can no longer be any summation of their neural excitations, the two regions must be completely separated. In this experiment the pulses occurred at a rate of six per second. An amplitude modulation at this rate produces a broadening of the frequency of twofold, so that the frequency band is 12 cycles wide.

This sort of sharpening of excitation in the nervous system can readily be demonstrated for vision, as Mach has pointed out (*cf.* page 418). Here it is called visual contrast, and often it shows itself over the entire visual field. The illumination of a small spot on the retina produces a marked reduction in sensitivity in the remaining areas. This nerve action makes the retinal image appear to be much sharper than it actually is. Thus the large amount of stray light that is present within the eye is largely inhibited through contrast (Tschermak-Seysenegg). This can be shown by throwing a bright beam of light on the blind spot. This spot is not seen, but nearly the whole visual field glows with stray light. The experiment can be carried out in a darkened room with two points of light placed horizontally about 50 to 60 mm apart. If now the right eye is closed and the left eye is fixated on the point

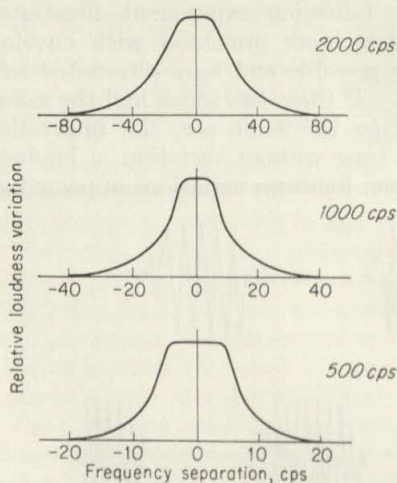


FIG. 13-5. Magnitude of loudness variations produced by alternating pulses of different frequency, plotted as a function of the frequency separation for 2000, 1000, and 500 cps. The pulses were presented at a rate of six per second.

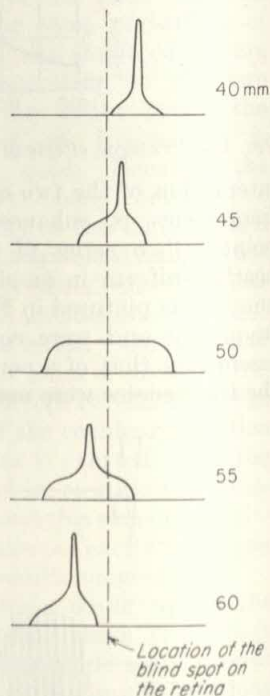


FIG. 13-6. Sensory effects obtained by illuminating the retina and the blind spot with a point source of light.

on the right from a distance of about 20 cm, then the point on the left will give a strong illumination of the blind spot and will not be seen. If now there is a slight change in the separation of the two points so that this point becomes visible, the stray light is markedly reduced. Figure 13-6 shows how the spatial distribution of the light intensity varies as the distance between the two points is gradually increased. At a distance of 50 mm the image of the bright point falls on the blind spot.

However, this phenomenon of contrast is not restricted to the sense organs. It is even more prominent as a general characteristic of the

neural pathways, in the blocking of weak excitation by the nerves that are carrying stimulation. A similar mechanism of the nervous system accounts for the fact that a person is unable to think of two different things at the same time.

CURRENT STATUS OF THEORIES OF HEARING*

The words "theories of hearing" as commonly used are misleading. We know little about the functioning of the auditory nerve and even less about the auditory cortex, and most of the theories of hearing do not make any statements about their functioning. Theories of hearing are usually concerned only with answering the question, how does the ear discriminate pitch? We must know how the vibrations produced by a sound are distributed along the length of the basilar membrane before we can understand how pitch is discriminated, and therefore theories of hearing are basically theories concerning the vibratory pattern of the basilar membrane and the sense organs attached to it.

The problem under discussion is a purely mechanical one, and it may well seem, at least to the layman, that it can easily be solved by looking at the vibratory patterns in the cochlea. Unfortunately, this direct approach proves difficult, for without stroboscopic illumination and other special devices, it is hardly possible to observe any vibration in the nearly transparent gelatinous mass in the cochlea of a living organism.

Various Vibratory Patterns of the Basilar Membrane. Reports of the various vibratory patterns of the basilar membrane that have been proposed thus far are to be found in textbooks on the psychology of hearing.† These reviews point up the differences between the various hypotheses, and some of them are highly critical. Indeed, they are so critical that they give the impression that the psychology of hearing is nearing the end of its productive period and entering a phase of unconstructive criticism. It is desirable to show, therefore, how the various theories of hearing are interrelated, and how by manipulating two independent physical variables of the basilar membrane—its absolute stiffness and the coupling of adjacent parts—it is possible to obtain a continuous series of vibratory patterns each group of which is in agreement with one of the four major theories of hearing. We may proceed continuously from curves predicted by the resonance theory to curves predicted by each of the other three theories in turn. It is thereby shown that the various theories form one continuous series of vibratory patterns. The question is then, how is the basilar membrane displaced and how does it move during a sinusoidal vibration of the ossicles?

Although the movement of a membrane depends on other factors as well, we shall turn our attention first to the elastic properties of membranes. Three elastic properties of the membrane in a cochlear model

* Article 76 as listed in the Author's Bibliography. Published in 1956.

† See Stevens and Davis, Wever (3), Ranke (6), Wever and Lawrence (3), and Ruch (3).

can be varied: the absolute value of stiffness, the slope of stiffness along the length, and the coupling between adjacent parts.

1. The absolute value of the stiffness of the membrane can be changed. If the membrane is stiff, a pressure difference across the membrane causes only a small displacement or deformation.

2. The stiffness of the membrane can be constant, or it can vary along the whole length. The basilar membrane is stiffer near the stapes than it is near the helicotrema; for man and most other vertebrates, the stiffness near the stapes is about a hundred times greater than it is at the other end.

3. The coupling between the adjacent parts of the membrane can be varied. In a membrane made of thin elastic fibers stretched across a frame, it is clear that if there is no coupling between one strand and its

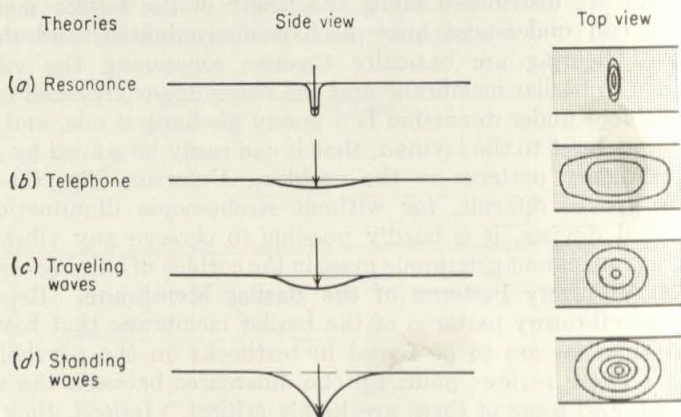


FIG. 13-7. Patterns of deformation produced in different kinds of membranes on applying force at a point. The membranes have different characteristics according to the four theories as indicated.

adjacent strands, each strand can vibrate independently. The strands can be coupled by a thin sheet of rubber placed along the whole set. Then the coupling becomes greater as the thickness of the rubber sheet is increased. A membrane can also be made of a smooth sheet of rubber alone, without individual strands.

These three possibilities can be expressed mathematically by saying that we have three independent variables for the elasticity of the membrane. There are two methods for investigating the effect of manipulating these variables on the vibratory pattern of a membrane. First, we can calculate the vibrations. Unfortunately this is a time-consuming job. Or second, we can construct a model of the cochlear membrane and vary its elastic properties. The author has made life-size models of the human cochlea and models that were larger. The enlarged models were constructed in the same way that full-scale ships are constructed from small-scale models. As is well known, this kind of dimensional enlargement has proved highly successful.

Figures 13-7 and 13-8 show some of the effects obtained by varying the elastic properties of the membrane. Figure 13-7a shows a small section of the membrane model consisting of coupled strands acted on by a point force (needle tip). The absolute value of the elasticity of the different strands varies continuously from 100 to 1 from left to right along the membrane. Seen from the top, the deformation pattern is a group of elongated ellipses, the deformation spreading neither to the left nor to the right. The side view shows this limited lateral spread more clearly. This model simulates the system of almost freely vibrating elastic resonators that is postulated by the resonance theory of hearing. If we immerse this membrane in fluid, the vibratory pattern seen in Fig. 13-8a is obtained for a steady tone.

With the same slope of elasticity and the same driving frequency, but with an increase in the absolute value of the membrane stiffness, a steady tone causes the whole membrane to vibrate in phase (all parts of the membrane reaching their maximal elongation simultaneously), in the manner of a telephone diaphragm, as shown in Fig. 13-8b. This is the pattern of vibration assumed by the telephone theory of hearing. The vibratory pattern for the steady tone is independent of the coupling between adjacent parts of the membrane because the whole membrane vibrates in phase, with no force acting laterally. Because of the increase in stiffness, the same point force that was used before now produces a smaller deformation (Fig. 13-7b). If the rubber strands are replaced by a flat plastic sheet that is stretched and clamped along the two long sides of the frame of the model, the point force produces the same lateral spread.

We obtain substantiation of two other types of hearing theories simply by decreasing the thickness of the elastic sheet. As the thickness decreases, the maximal amplitude of the displacement becomes greater. When the thickness of the sheet is decreased slightly, the same steady tone produces a traveling wave moving away from the source as in Fig. 13-8c. The corresponding deformation by a point force is shown in Fig. 13-7c. When a thinner sheet is used, the same point force pushes the partition out still farther; and the same steady tone produces traveling waves that become shorter and travel farther until some are reflected from the end of the membrane and standing waves result as in Fig. 13-8d. The standing-wave theory was proposed by Ewald.

A change in the frequency of a steady tone moves the maximum of the vibrations along the basilar membrane, as the resonance theory assumes.

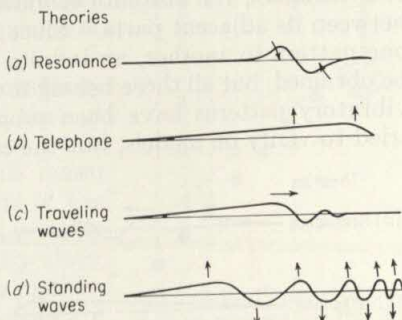


FIG. 13-8. Patterns of vibration produced in different kinds of membranes by a continuous tone, with normal damping. The arrows indicate the direction of motion at a given instant.

An increase in frequency moves the maximum toward the stapes. The resonance theory of hearing is a place theory in which pitch discrimination depends on locating the place along the membrane that is set in maximal vibration. According to the telephone theory, a change in frequency need not affect the displacement of the membrane, and pitch discrimination depends on some unknown function of the brain. The traveling-wave theory is also a place theory, for an increase in the frequency moves the maximum of the vibrations toward the stapes and a decrease moves it toward the helicotrema. According to the standing-wave theory, an increase in frequency increases the number of nodes and decreases the distance between them. The brain uses this information to determine pitch.

As may be seen in Fig. 13-8, four basically different vibratory patterns can be obtained for a steady sinusoidal tone simply by manipulating two variables, the absolute stiffness of the membrane and the coupling between its adjacent parts. Since it is possible to go continuously from one pattern to another, an infinite number of intermediate patterns can be obtained; but all these belong to a single family of curves. Additional vibratory patterns have been proposed, some of which the writer has tried to verify on models, but the conclusion has been reached that they

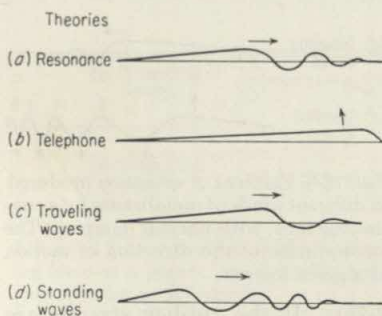


FIG. 13-9. Patterns of vibration in membranes during the transient stage, with normal damping.

are only drawings and have no physical existence. Figure 13-8 shows all the principal patterns that there are.

We have seen how, for a continuous tone, it is easy to substantiate each theory in turn simply by manipulating the elastic properties of the membrane. The differences among the theories depend wholly on the sizes of these variables. It is even more surprising, however, to find that for transients—for example, the onset of a steady tone—the differences

between the resonance, traveling-wave, and standing-wave theories disappear completely, despite the emphasis that these differences have received. Traveling waves develop during the onset of vibrations in membranes whose vibratory patterns are described by these three theories, as shown in Fig. 13-9. (The driving frequency is the same as in Fig. 13-8.) Only the telephone theory assumes that all parts of the membrane vibrate in phase, in complete conformity with the movements of the driving stapes.

It is especially difficult to understand how in a system of free resonators the onset of a continuous tone produces traveling waves. A simple experiment was set up to demonstrate the occurrence of traveling waves in a system of free resonators as shown in Fig. 13-10. A pendulum with a large mass was clamped to a long horizontal driving rod from which a

series of small pendulums was suspended. The lengths of the pendulums increased continuously from one end of the system to the other, from right to left in the figure. One pendulum in the middle of the series was of the same length as the heavy driving pendulum. During continuous oscillation of the driving pendulum, the resonant pendulum was set in motion by small movements that were transmitted through the oscillating supporting rod. A change in the period of the driving pendulum made a different pendulum resonate. Thus the series was a system of free resonators, each of which resonated at a different frequency. The onset of the oscillations of the driving pendulum set in motion a large section of the system, and a traveling wave was observed moving toward the longer pendulums, as can be seen in the sequence of film shown in Fig. 13-11.

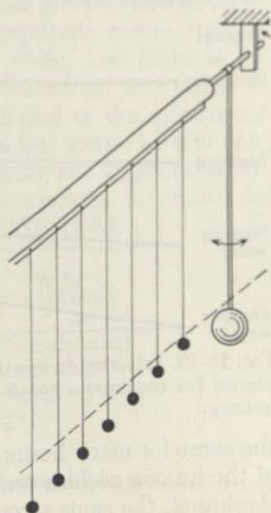


FIG. 13-10. System of pendulums representing free resonators.

To complete this survey of the various hearing theories, it should be mentioned that at very low frequencies the movement of a vibrating system is independent of its mass; the displacement of the various parts of the membrane is determined solely by their elasticity. Since the slope of elasticity along the membrane is the same in all four models, the vibratory patterns for low frequencies are similar, as shown schematically in Fig. 13-12. The largest excursions appear in the standing-wave model, which has the most yielding membrane. Another factor that affects the movement of the basilar membrane is the damping provided by the fluid in the cochlea. In the models, when the viscosity is high, the differences between the various theories tend to disappear. When the fluid friction is extremely high, the movements of the membrane

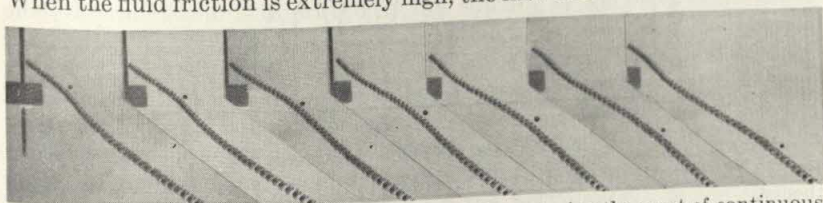


FIG. 13-11. Series of views of the system of pendulums during the onset of continuous sinusoidal movements. A traveling wave moves from left to right.

are determined solely by the frictional forces in the fluid, independent of the elasticity values of the membrane. Here again the vibratory patterns are identical for all the theories, and even the displacements are equal (see Fig. 13-13).

According to the foregoing discussion, the question of which hearing theory is valid reduces to the more easily answered question, what are

the numerical values of the elasticity and coupling along the basilar membrane? In these experiments, when the tip of a needle was pressed perpendicularly on the surface of the basilar membrane of some lightly anesthetized vertebrates (guinea pig, mouse, cat, and pigeon), the resulting deformation was almost circular; both the top and side views were identical with Fig. 13-7c. The shape of the deformation remained

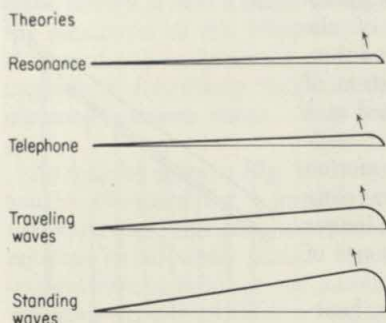


FIG. 13-12. Patterns of vibration in membranes for continuous tones of low frequency.

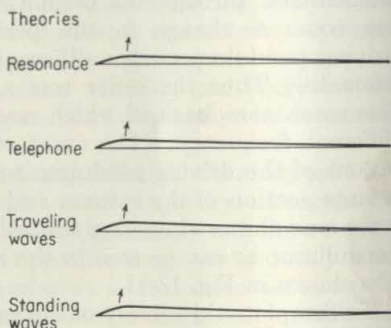


FIG. 13-13. Patterns of vibration in membranes immersed in fluid of high viscosity, when exposed to continuous tones.

the same for many hours after the death of the animal. In preparations of the human cochlea and the cochleas of large animals such as cows and elephants, the same circular deformation was found. The shape of the deformation proves that the coupling between the adjacent parts of the basilar membrane is so large that it invalidates the resonance theory of hearing.

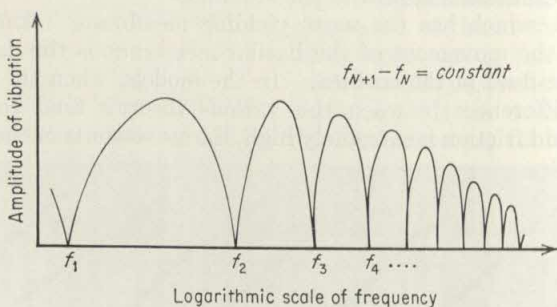


FIG. 13-14. Hypothetical audiogram according to the principles of the standing-wave theory.

The side view of the deformation makes it clear that the stiffness of the basilar membrane is too great for standing waves to occur. The formation of standing waves along the basilar membrane is improbable also because standing waves with large amplitudes occur only at certain frequencies; if standing waves were to occur, the sensitivity of the ear would undergo large fluctuations during a continuous change in frequency. Figure 13-14 shows the type of audiogram that would be

obtained under these conditions. Thus it is clear that the vibration of the basilar membrane cannot be accounted for by either the resonance theory or the standing-wave theory.

Observations of the basilar membrane in mammals substantiate the traveling-wave theory. Under stroboscopic illumination, a steady tone of 1000 cps produces traveling waves similar to those pictured in Fig. 13-8. When the frequency is lowered, the maximal amplitude moves toward the helicotrema (toward the right side of Fig. 13-8), and there is an increase in the length of the membrane that is vibrating practically in phase. The place of the maximum reaches that end of the membrane in the different animals at the following frequencies: mouse at 400 cps, pigeon at 80, rat at 180, guinea pig at 200, man at 30, and elephant at 30. Below these frequencies the basilar membrane vibrates in phase, as postulated by the telephone theory, as shown in Fig. 13-8b.

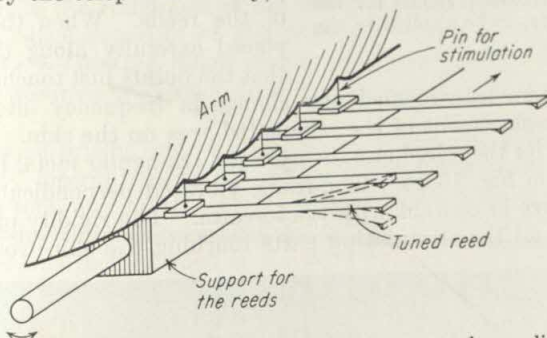


FIG. 13-15. Mechanical model for the resonance theory, to be applied to the skin of the arm.

Below the critical frequency, pitch discrimination depends entirely on the temporal sequence of stimulation of the nerves. Above the critical frequency, there is a second factor, the shifting of the place of maximal stimulation along the basilar membrane. We must now ask whether pitch discrimination is improved by this shifting of the place of maximal stimulation as compared with the conditions under which it depends wholly on the temporal sequence of the vibrations. The problem is no longer mechanical, but one of how the nerves react to different vibratory patterns on the basilar membrane.

Mechanical Models of the Cochlea. In order to investigate this aspect of the problem, cochlear models were constructed in which the skin of the forearm was substituted for the nerve supply of the basilar membrane. Three mechanical models were made that stimulated the skin of the arm in accordance with the three vibratory patterns in Fig. 13-8a, b, and c. No model with standing waves was built because change in frequency would produce a large change in amplitude, and consequently it would be difficult to distinguish amplitude changes from frequency changes (which is not true for the ear). The mechanical model for the resonance theory is shown in Fig. 13-15, for the telephone theory in Fig. 13-16, and for the traveling-wave theory in Fig. 13-17.

The resonance model consisted of a series of tuned steel reeds attached to a metal support that oscillated slightly around its longitudinal axis. The length of the support was equal to the length of the forearm. Thirty-

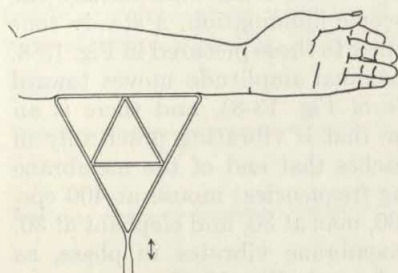


FIG. 13-16. Mechanical model for the telephone theory, to be applied to the skin of the arm.

six reeds, tuned in equal intervals over a range of two octaves, were distributed along the whole length. A small pin on each reed, fastened close to the support, touched the surface of the skin of the arm. The pins had rather small points, so that the skin would not pick up too much energy from the vibrating reeds; otherwise it would not have been possible to obtain a sharp resonance of the reeds. When the arm was placed carefully along the pins, so that the points just touched the skin,

the reed system transformed any change in frequency into an easily observable displacement of the stimulated area on the skin.

The model for the telephone theory was a triangular metal frame made of tubing as in Fig. 13-16. The frame vibrated perpendicularly to the axis of the edge in contact with the forearm. The rigidity of the frame ensured that all the stimulating parts touching the skin would vibrate

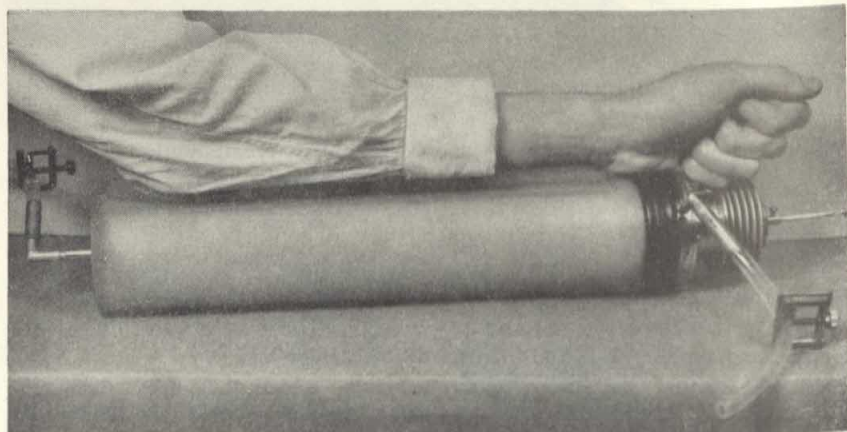


FIG. 13-17. Mechanical model for the traveling-wave theory, to be applied to the skin of the arm.

in phase. From time to time, phase constancy along the frame was verified by stroboscopic illumination.

The model for the traveling waves was a section of a model of the human cochlea, enlarged by dimensional analysis. The frequency range was two octaves. The model was a plastic tube cast around a brass tube with a slit. The tube was filled with fluid. Figure 13-17 shows the position of the arm on the vibrating membrane. A vibrating

piston set the fluid inside the tube in motion, and forces in the fluid produced waves that traveled from the hand to the elbow. The traveling waves thus produced were similar to those observed in preparations of the human cochlea. The maximum amplitude of vibration was rather broad, and when it was observed under stroboscopic illumination, it moved along the membrane as the frequency was changed. Although the maximum was flat as it moved along the arm, the sensation of vibration was concentrated on a relatively short length (about 2 to 4 cm); hence, any frequency change was easily recognized by a shift in the stimulated area. Seemingly the nerve network in the skin inhibits all the sensation to either side of the maximum of the vibratory amplitude, thereby producing a sharpening of the stimulated area.

If we compare the three models, we find that the difference limen for "pitch" discrimination below 40 cps is the same because the skin is able to discriminate the roughness of the vibrations as such. But for higher frequencies, displacements of the sensation along the arm produced by either the resonating model or the traveling-wave model permitted much more accurate frequency discrimination than the telephone-theory model does.

The most surprising outcome of these experiments with models was that "pitch" discrimination did not deteriorate when the presentation time of the tone was short. Even when the stimulus was only 2 cycles, the "pitch" discrimination for both the resonance model and the traveling-wave model was just as good as it was for a continuous tone of longer duration. Closer examination showed that in both models the place of maximal amplitude was determined during the first two cycles of the onset of a tone. Figure 13-9 shows that for transients there is little difference between the vibratory patterns of the resonance and traveling-wave theories. In both, waves travel over a long section of the vibrating system. The surprising fact is the inhibitory action of the nerve supply, which suppresses all sensation except on a small spot near the maximal amplitude of vibration. In the ear the situation seems to be the same because there also 2 cycles of a tone are enough to enable us to discriminate the pitch of a tone.

HUMAN SKIN PERCEPTION OF TRAVELING WAVES*

According to many books on hearing, our present knowledge of pitch discrimination in the cochlea consists of a large number of theories and an almost equal number of experimentally reproducible facts. Confronted with this situation, an investigator has two choices. He can concentrate on the common elements among the facts and ignore the apparent discrepancies, or he can place his emphasis on the differences between the theories and conclude that, in spite of the intricate structure of the organ of Corti, the task of pitch discrimination should be attributed to the brain.

* Article 74 as listed in the Author's Bibliography. Published in 1955.

Everyone will agree that the discrepancies ought to be pointed out, for nothing is more welcome than really incisive criticism; but certainly it seems that in the specific case of pitch discrimination in the last fifty years these differences have been overemphasized. This overemphasis can be illustrated by one example.

In general, the resonance theory of hearing and the theory that assumes the existence of traveling waves along the basilar membrane are described as two theories of pitch discrimination that have nothing in common. Details of the differences between the two theories are so clearly set forth in most handbooks that there seems no room for doubt. The writer decided, however, that for his own satisfaction he would like to verify the existence of these differences experimentally. For this purpose a set of tuned reeds was used (Hartmann-Kempf). These reeds were

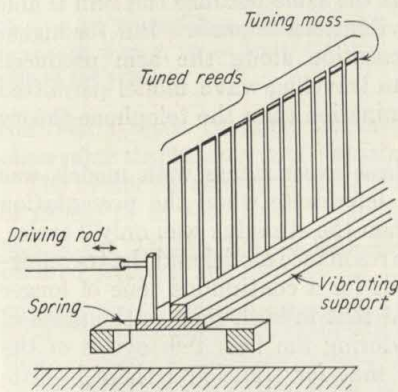


FIG. 13-18. A tuned-reed system.

fixed in a common support and set in vibration around its longitudinal axis by an electromagnetic driving system (see Fig. 13-18). The reeds were vibrating completely free; they were tuned so that their resonant frequencies decreased continuously from left to right. When the common support was in continuous sinusoidal vibration, only three or four reeds of the set had large amplitudes, whereas all the other reeds stood still. When the driving frequency was lowered, the point of maximal vibration moved toward the reeds that had been

tuned to the lower frequencies. As shown in Fig. 13-18, the maximum point moved to the right. Every frequency put a different small section of the set of reeds in motion, thus illustrating the localization of the stimulus along the basilar membrane according to the resonance theory of hearing, as described in the handbooks. The vibratory patterns of the set of reeds seemed to have nothing in common with traveling waves even when observed under stroboscopic illumination.

In the search for more details, a motion picture was taken of the set of reeds at a speed of about 1800 frames per second and projected a hundred times slower, that is, at 18 frames per second. It was surprising to find that when continuous vibrations were suddenly applied to the system the result was a traveling wave that moved from the stiffer part of the reed system (corresponding to the stapes side of the cochlea) to the more flexible part (corresponding to the helicotrema). Such a traveling wave can be seen in Fig. 13-19a. The series of exposures begins at the left, with a time interval of $1/1800$ sec between successive exposures. One particular reed has been marked by a dot in each exposure to show the movement of the wave. (Compare the position of the bulges with the row of dots.) The amplitude of the waves can be seen moving from

left to right. It goes through a maximum and then decreases abruptly. In Fig. 13-19*b* the interval between exposures remained the same, but the photographs were made after the reed system had been vibrating continuously for some time. The amplitudes are larger, but they spread over only a small number of reeds and show the typical vibratory pattern of a resonant system with the reeds on either side of the resonance point moving in opposite phase. There is no lateral spread in the over-all pattern of vibration.

The slightest change in amplitude or frequency of the driving force immediately produced traveling waves along the reeds, if the changes in amplitude and frequency were aperiodic. The question now is, which

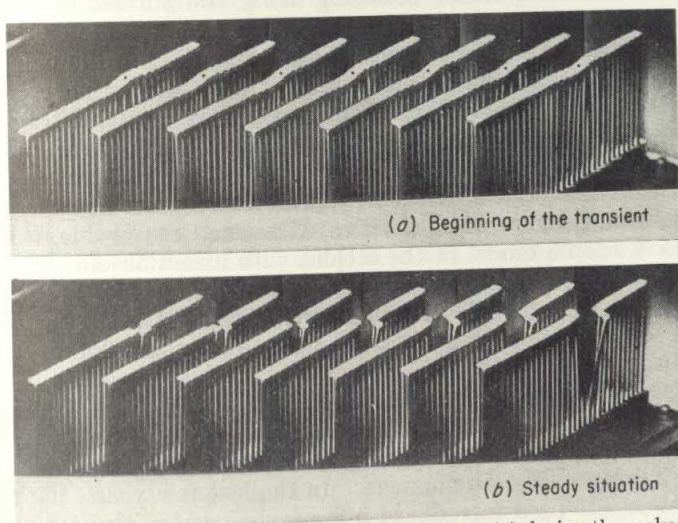


FIG. 13-19. Two series of views of the tuned-reed system, (a) during the early transient period and (b) during the steady state. The series run from left to right.

is more important for hearing, the transients or the steady state? If transients are important, we shall have to take traveling waves into account even when we are considering resonance theories of hearing. Certainly transients are important for the recognition of speech, which consists of a continuous change in frequency and amplitude. In music we have the same situation. Backhaus (3) showed that it was not possible to discriminate between a flute and a violin on a recording in which the transients had been masked out.

Furthermore, we have to take into account the fact that, in the central nervous system, the switching on or off of a tone produces marked potential changes. Yet it is difficult to find a potential change that can be correlated with a continuous tone. This situation seems to point up again the importance of transients. There is then a large overlap between the resonance theory of hearing and the theory of traveling waves.

It seems likely that in the future more attention will be paid to the common elements in these different views, not only in respect to the particular question of pitch perception, but also in the whole field of sensory perception. All the sense organs with large surface areas, such as the eye, the skin, the tongue, and the basilar membrane, show striking similarities in the way in which they make spatial discriminations. The neural pathways are similar. In every one of these sense organs the receptors, which are spread along the surface, send single nerve branches to the higher centers. There is, in addition, a layer consisting of a large number of lateral interconnections between the ascending nerve branches. This layer, called a plexus, is probably responsible for the inhibitions and facilitations occurring along the surface of the sense organ. If we can learn how the plexus works in one sense organ, there is a good chance that this knowledge can be applied to the other sense organs. For example, an understanding of the contrast phenomena of the retina would probably help us to understand the inhibitory effects along the basilar membrane that must be present in order to account for the sharp discrimination between different vibratory patterns.

Of all the sense organs, the skin appears to be most like the cochlea from the evolutionary point of view. It seemed reasonable, therefore, to try to develop a model of the cochlea with a section of skin as sense organ. Several inhibitory effects observed in the cochlea are probably found in the skin model. Furthermore, it should make possible an isolation of those functions that the more highly developed organ of Corti can perform and the skin cannot.

Mechanical Model of the Cochlea. In applied physics, dimensional models have been used extensively and successfully as research tools. In addition to dimensional models, demonstration models have been built to illustrate some phenomena. In the last few years, the concept of the model has been introduced into psychology, so that we now find descriptions of such concepts as mathematical or statistical models of behavior. The models of the cochlea that the writer has used belong in the group of dimensional models. These models are built according to rules developed from dimensional analysis and permit the measurement of data that would otherwise be difficult to calculate. The dimensional models contain more data than we have information on, and for this reason are highly successful in research. Demonstrational models, on the other hand, are not built according to model laws or any other type of general rule and therefore demonstrate only specific features. Let us illustrate the differences between the types of models.

If a precise replica of the cochlea is made but the cochlear partition is made unusually stiff, all the sections of the cochlear partition will move in the same way. This model would be a demonstrational model of the telephone theory of hearing (Rutherford). If the cochlear partition in the model is made very flexible, we shall find a large number of standing waves along the cochlear partition. This type of model demonstrates the auditory theory of Ewald (2). To obtain a dimensional model of the cochlea, it is necessary to measure the elastic properties of

the cochlear partition and to use these properties in the construction of the model. In this type of model, traveling waves are seen that are of exactly the same type as those observed in the cochlea of the living guinea pig. The model can be enlarged, and, if the enlarging is done according to the model laws, no change in the vibratory pattern of the cochlear partition will be observed.

For present purposes a dimensional mechanical model was used. Diestel (1) had already constructed a model of the size required, and his measurements were useful in the construction. In the first attempt to produce an enlarged model of the cochlea using living skin as the series of end organs, a fresh piece of frog skin was stretched across a longitudinal frame and fitted into a model. Such a model can be kept functioning for a day. Unfortunately, the frog skin proved to be about as complicated electrophysiologically as the organ of Corti.

When the model with the frog skin proved unsatisfactory, a new model was constructed in which a metal tube with an internal diameter of 5.5 cm and a length of 30 cm was used to represent the vestibular canal of the cochlea. One end of the tube was closed and the other end was attached to a vibrating piston. The tube was filled with water. Along the whole length of the metal tube a small slit was cut. The arm of the observer was placed on the slit, the skin of the arm making a watertight seal. The width of the slit was adjusted so that the volume displacement of the skin surface corresponded (according to the model laws) to the volume displacement of the basilar membrane of the human ear. In this type of simplified model only the vestibular canal of the cochlea was represented. Earlier measurements showed that in this simplified cochlear model the essential features of the vibratory pattern of the elastic membrane are the same as in the unmodified model with both canals (page 439).

In the frequency range between 30 and 100 cps, the continuous vibration of the piston produced a sensation of vibration in a restricted area about 5 to 8 cm long. When the frequency was increased, this area moved toward the piston, where the width of the slit was small. A lowering of the frequency moved the sensation to the more distant side. Besides the sensation of vibration, a gentle pressure—such as a small jet of air might produce—was felt on the skin. A change in the frequency that was continuous but not too slow produced an increase in the intensity of the pressure sensation, because the skin at the place where the pressure was applied adapts more quickly to the pressure than to the sensation of vibration.

It soon became evident that this type of model should be used for the final observations, but that it was too tiring for the initial orientations. In addition to the fact that the water in the tube had to be kept at 37°C, every change in the tension of the arm muscle changed the volume elasticity of the skin surface, as a consequence of which the vibratory pattern was displaced.

To avoid this difficulty, the vibratory pattern was fixed by a special membrane and the vibrations of the membrane transmitted through a

coupling system to the changing impedance of the arm. If the coupling was loose, the vibratory pattern of the membrane remained constant, even with a change in the loading.

A cross section of the model is seen in Fig. 13-20*a* and *b*. A plastic tube was cast around a brass tube with a slit. The width of the slit

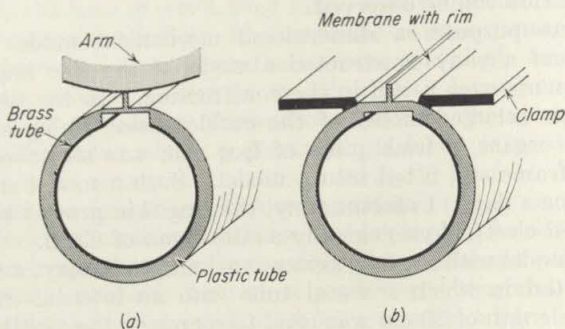
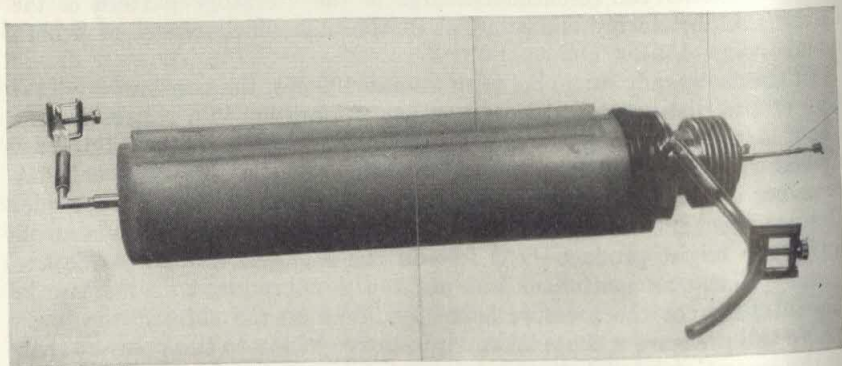


FIG. 13-20. Two cross sections of a dimensional model of the cochlea, (*b*) made near the driving end and (*a*) made near the other end.

was constant, and the elasticity of the membrane was changed by altering its thickness, as a comparison of Fig. 13-20*a* and *b* shows. To the middle of the membrane, a ridge was affixed on which the skin of the arm rested. The ridge was 3 mm wide, which was small enough to produce the desired loose coupling between the arm and the membrane. In some of the

Membrane with edge

Bellows



Plastic tube

FIG. 13-21. Detailed view of the model.

experiments, a steel table was placed on both sides of the membrane to form a rest for the arm. This table was used also to press the edge of the soft part of the plastic tube against the brass tube.

A photograph of the model represented in Fig. 13-20*a* is shown in Fig. 13-21. Two rubber strands were used to clamp the right end of

the plastic tube to the brass tube. A bellows made of thin metal was inserted into the right side of the tube. This bellows was compressed and expanded by the attached vibrating rod, which set the fluid column in the canal in motion.

The width of the membrane was kept constant along the entire tube, so that the volume displacement of the membrane was proportional to the displacement in the middle of it. The reciprocal values of the amplitude of the membrane along the tube for vibrations of 2 cps are given in Fig. 13-22 and represent the stiffness of the membrane. For so low a frequency, the alternating pressure on the surface of the membrane is constant for the whole length of the tube. The arm was placed along the rim above the membrane as shown in Fig. 13-17. Most of the effects could be observed even when the arm was covered by a sleeve.

Frequency Localization along the Membrane of the Model. When the bellows on the end of the tube in the model was set into sinusoidal

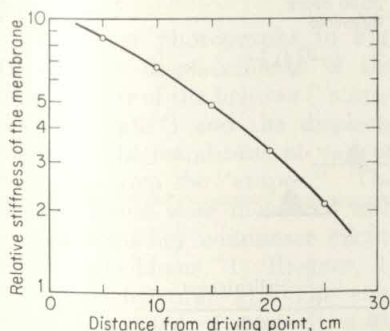


FIG. 13-22. The variation in stiffness along the membrane of the model.

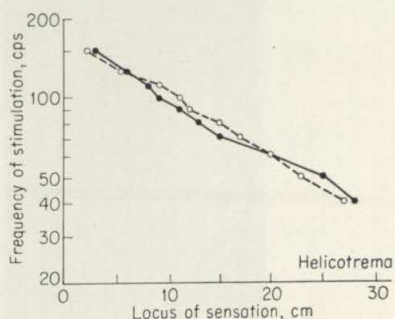


FIG. 13-23. The locus of the sensation as a function of frequency of vibration.

vibration, traveling waves appeared along the membrane and the plastic ridge. They traveled from the stiffer section of the membrane to the softer section and could be observed easily under stroboscopic illumination. In the model with the elastic properties shown in Fig. 13-22, the maximum of amplitude distribution along the membrane was surprisingly broad, but it moved back and forth with changes in the driving frequency. When the observer laid his arm on the ridge of the membrane, only a small section of the membrane seemed to vibrate. He could point to the center of the field of vibration perceived. Its place depended to a certain extent on the way the arm was laid on the ridge. It was different for the lower and upper arm, and it often changed if the muscles were tensed or relaxed. Individual differences were great too, and the location changed with the intensity of the stimulus. In spite of all this, it was possible to map the relation between the frequency and the place of maximal perception. Figure 13-23 shows this relation for two successive sets of measurements on the left arm (with the hand close to the "stapes") at an intensity 25 db above threshold. The two sets are not very different. It should be noted that care was taken that the vibrating

ridge of the membrane touched the skin along its whole length without pressing on bone, because bone pressure produces a different type of sensation of vibration which is generally localized in the joints. Furthermore, care had to be taken to prevent the transmission of cues by means of the ear. The whole driving system was acoustically insulated, and the auditory meatus was closed with an earplug and covered by an earphone case so that no sound could be detected. These precautions are important for every type of observation of sensations on the skin.

As can be seen from Fig. 13-23, in the model just described the frequency band of two octaves (40 cps to 160 cps) was spread over 26 cm.

One of the long-standing problems of hearing is the question of how the ear determines the pitch of tone pulses when their duration is only 1 or 2 cycles. For such pulses the frequency spectrum is so broad that no sharp physical localization along the membrane can be expected.

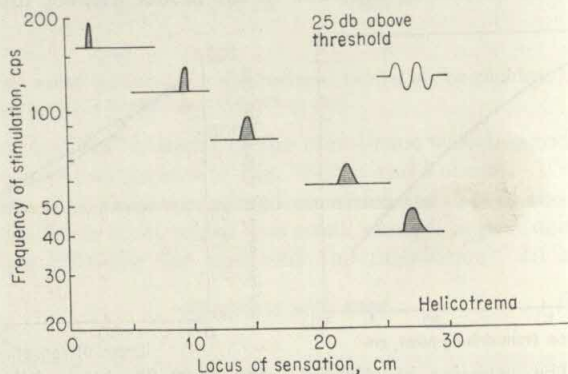


FIG. 13-24. The perceived extent of the sensation as a function of frequency, for a pulse of two waves.

Experiments with the model show that the decrease in the number of cycles of the tone had no deteriorating effect at all on the sharpness of the localization felt on the skin. On the contrary, many subjects reported a definite shrinking of the area in which the vibrations were felt. To demonstrate this, a sinusoidal tone pulse 25 db above the threshold of sensation with a length of two full-waves was presented to the arm. The spread of the sensation along the membrane as reported by one subject is shown in Fig. 13-24. For 160 cps this spread was only about 0.5 to 0.8 cm. For 40 cps it was about four times as long, and it had a sort of tail in the direction of the "helicotrema." Here again the location and spread of the sensation varied with the way in which the arm was applied to the ridge, but by and large the same picture was obtained on different days and by other subjects as well.

In general, for continuous tones the spread was larger. For some subjects it was as much as five times larger, especially for the lower frequency range. But several observers reported practically no change in the amount of spread between short tone pulses and a pulse of one or two

sine waves. This situation adds new interest to the old problem of pitch discrimination for short tone pulses.

The physical part of the transients in the model may be described as follows. In the production of the tone pulses, an electronic counter, similar to the type used in measurements of radioactivity, was used to count the number of cycles. Coupled with an electronic switch, it permitted turning the generator voltage on or off at exactly the moment the voltage went through the zero point. The top photograph in Fig. 13-25 shows the current sent through the driving unit when the electronic counter was set for 2 cycles.

The lower photographs in Fig. 13-25 show displacements of the front surface of the bellows ("stapedial footplate") and the displacements of the membrane at various distances from the "stapes." The displacements were measured with a high-frequency condenser microphone (Backhaus, 1; Riegger, 1; F. Trendelenburg, 1). The condenser consisted of a small metal plate held parallel to the surface of the membrane, which had been painted with aluminum paint. A displacement of the membrane changed the capacity of the condenser and thereby changed the

radio frequency of an oscillator, thus permitting the observation of the momentary value of the capacity of the condenser on an oscilloscope.

The photographs in Fig. 13-25 show that the transients in the membrane were small. Only after the traveling waves passed the point of maximal amplitude did larger transients appear. We have to take into consideration, however, the fact that this model was relatively short—only two octaves long—and that under these circumstances there were reflections at the end of the model that lengthened the transients. This would not occur in a longer model, where there would be space enough to allow the waves to run out and be damped.

From these photographs we see that the cochlea transmits as short a tone pulse as 2 cycles to the place of maximal vibration without much distortion, and simultaneously produces even in this short time an amplitude distribution along the membrane that is hardly different from the amplitude distribution obtained during continuous sinusoidal vibrations.

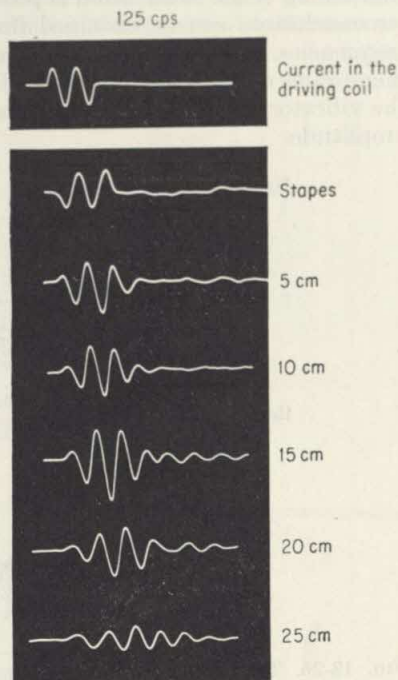


FIG. 13-25. The transients produced in the apparatus by a two-wave pulse, as a function of distance from the driving points.

Physically, therefore, the cochlea exhibits very short transients (*cf.* Jung). The amplitude distribution along the membrane is accordingly broad, so that from rough inspection there seems to be no contradiction between the transient time and the filtering action of the cochlea. The sharpening of the localization is produced by the nervous system. Similar conclusions can be obtained from beats produced by two different frequencies. Albert calculated the vibratory pattern of the basilar membrane during one full cycle of the beat and showed how quickly the vibratory pattern of the steady state is reached during the increase of amplitude.

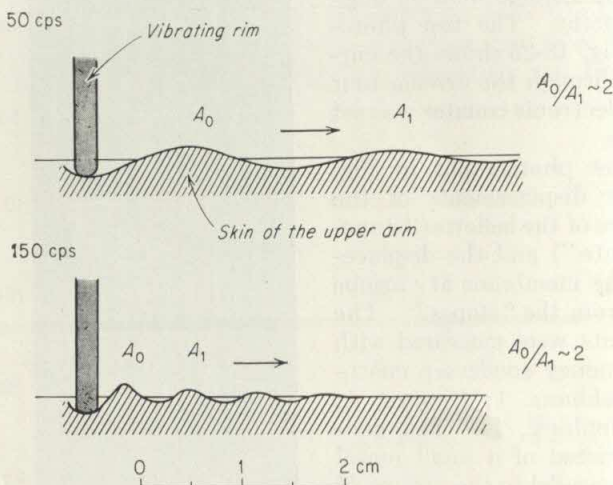


FIG. 13-26. The traveling waves on the skin of the arm at two frequencies of stimulation.

This sharpening of the spread of vibrations acts not only in the longitudinal direction of the membrane but in the lateral direction as well. The arm on the ridge of the membrane feels the lateral extent of the vibrations as about 1 cm wide. But if, with stroboscopic illumination, the movements of the skin surface were observed in the neighborhood of the ridge, waves were seen traveling away from the ridge in both directions for several centimeters, because the damping on the skin surface is small—of the order of 2:1 for two consecutive excursions in the same direction. Figure 13-26 shows stroboscopic observations on the upper arm. Besides the lateral spread of the stimulus, there was a spread in the deeper layers of the arm. If the muscles were relaxed and the bones were not touched, the sensation was localized on the skin surface.*

Figure 13-27 summarizes the action of the cochlear model with the skin as sense organ. In the upper drawing, the physical stimulus is

* Waves on the surface of the skin have been measured by Keidel (1) and Keidel and Schmidt.

shown as it developed on different points of the membrane when a sinusoidal vibration was suddenly started. The lower drawing shows how the sensation on the skin built up with time. The cochlea certainly represents a system that in the least possible time produces an amplitude distribution with a maximum. This maximum shifts along the membrane as the frequency rises. The inhibition of large areas of stimulation by the sense organ is a well-recognized phenomenon, and in the next section the effects on the skin are considered.

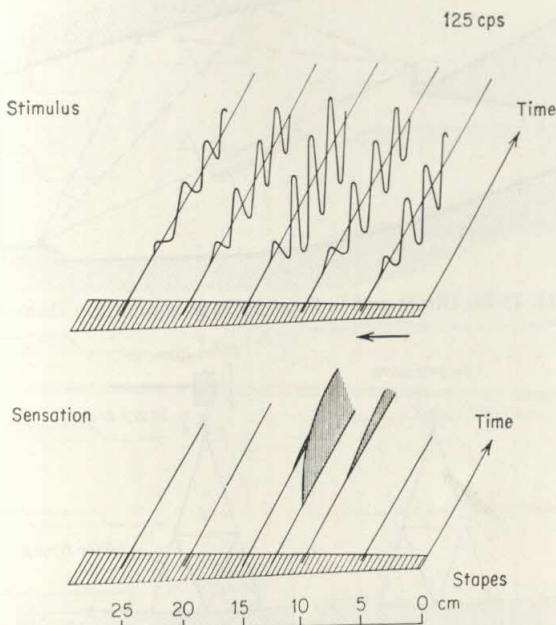


FIG. 13-27. Comparison of the stimulus waves along the skin of the arm and their perception for 125 cps.

Inhibitory Phenomena of the Skin. In life, inhibition is just as important as stimulation. It is highly developed in the ear and may be expected to be much the same in the skin from which the ear is formed. Without a highly developed inhibition, the ear would be inadequate in many situations. To demonstrate this, let us go into a theater. As can be seen from Fig. 13-28, the sound of the performer reaches the listener in a number of different ways. The direct sound (solid line) travels the shortest route and reaches the ears first. After that, a large number of echoes arrive (broken lines), as a rule after reflection from the ceiling. In many theaters the intensity of the echoes is equal to or even larger than that of the direct sound. If these echoes were not suppressed, the performer would seem to be located beyond the ceiling. Although suppression is more effective with both ears, it works well even with one.

In general, inhibition is strongest for a stimulus of brief duration and is much weaker for a sustained stimulus. The echoes of a click are easily suppressed by the ear. An analogous effect is found on the surface of the skin. A metal frame pressed slowly on the skin was felt along the whole length touching the skin (see Fig. 13-29). But if the frame was hit sharply with a hammer, a sensation was felt

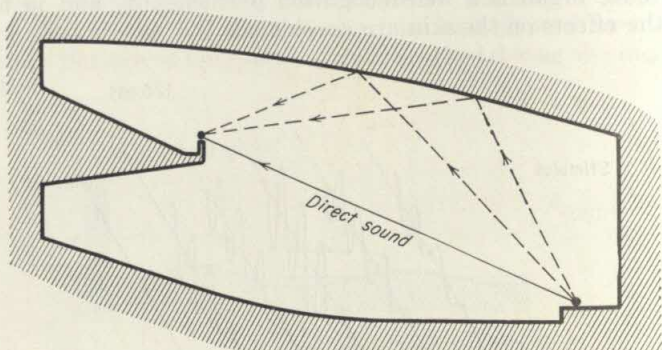


FIG. 13-28. Direct and indirect paths of sound in a theater.

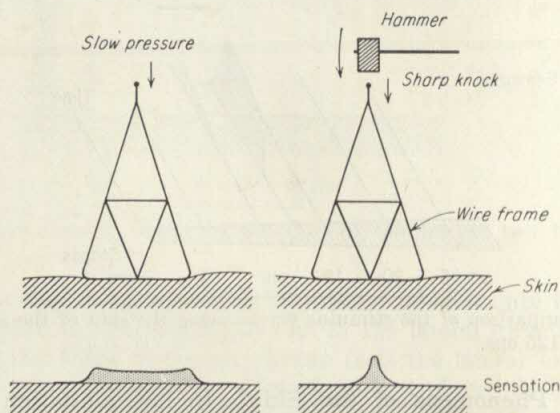


FIG. 13-29. Sensory effects produced by applying a stimulus slowly and abruptly to the skin.

only in a short section around the middle of the frame, as illustrated in the drawing on the right of Fig. 13-29.

To show how the duration of stimulation influences the inhibition, the same frame was attached to a driving unit that switched on a 100-cps tone for 2 cycles or more. The subjects were asked to make drawings indicating the approximate level of the "loudness" and the lateral spread of the sensation. The drawings made by one subject are shown in Fig. 13-30; other subjects had similar patterns. For presentations longer than 0.3 sec, the contour of the sensation approached the contour of the physical stimulus. The whole length of the side of the frame touching

the skin was 13 cm. The upper arm was used, and the amplitude of vibration was 6 db above threshold. In general, when the stimulation was continued for more than 10 sec, the sensation began to fall off in the middle part. After a while only the edges were felt to be vibrating, as shown in Fig. 13-31, until finally all sensation disappeared. Some observers reported that often, before the sensation disappeared completely, the locus of the sensation shifted back and forth between the edges and the center.

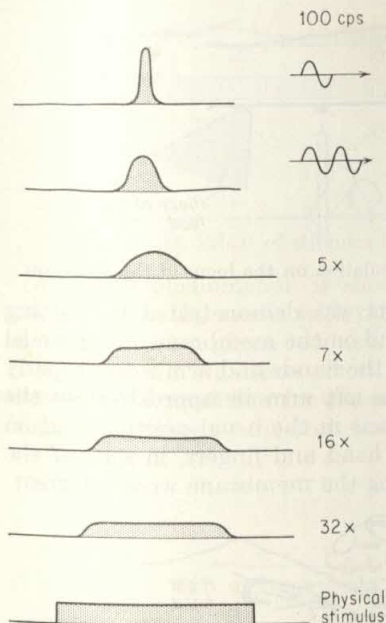


Fig. 13-30. Effect of applying vibratory stimuli of different durations to the skin over a line 13 cm long.

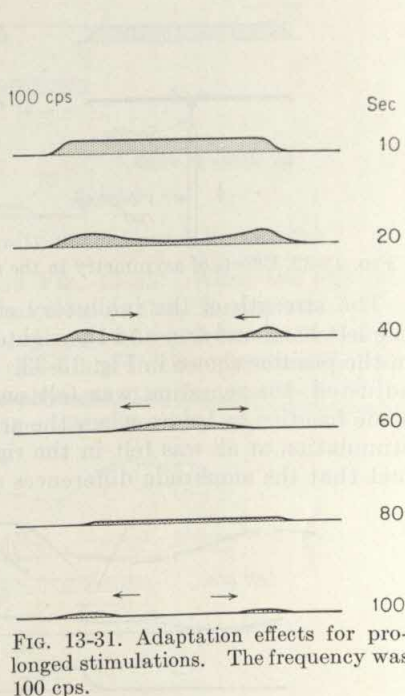


Fig. 13-31. Adaptation effects for prolonged stimulations. The frequency was 100 cps.

The maximum in the distribution of the amplitudes of vibration in the model is rather flat. It is interesting to see that even a slight change in the distribution of the amplitude along the surface can modify the locus of the sensation. The experiment shown in Fig. 13-32 shows this fact convincingly. To the vibrating rod driven by the electromagnetic system was attached a small perpendicular tube with a length of 13 cm. The perpendicular tube was pressed against the skin, and two full cycles of a 100-cps tone were presented. In this case, a small section in the middle of the tube seemed to vibrate as shown in the drawing on the left. By pressing a heavy piece of lead against one side of the vibrating tube, the maximum of the amplitude of vibration could be made to move slowly to one side. The place of sensation immediately shifted without much spread, as shown in the drawing on the right. These movements are sensitive near the center and slow down on the edges of the tubing.

An examination of the model of the cochlea by stroboscopic illumination showed that the various parts of the membrane did not vibrate in phase, but that as a consequence of the traveling waves there was a time delay between the movements of the waves in the parts close to the "stapes" and the parts farther away. The inhibitory effects may therefore be expected to be even stronger.

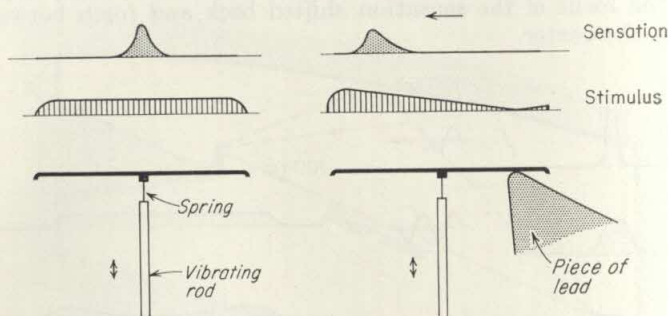


FIG. 13-32. Effects of asymmetry in the stimulation on the locus of the sensation.

The strength of the inhibitory effects was demonstrated by putting the left hand and arm and the right hand on the membrane of the model in the position shown in Fig. 13-33. If the hands and arm were properly adjusted, the sensation was felt on the left arm in approximately the same location as before when the arm was in the usual position; and no stimulation at all was felt in the right hand and fingers, in spite of the fact that the amplitude differences along the membrane were not great.

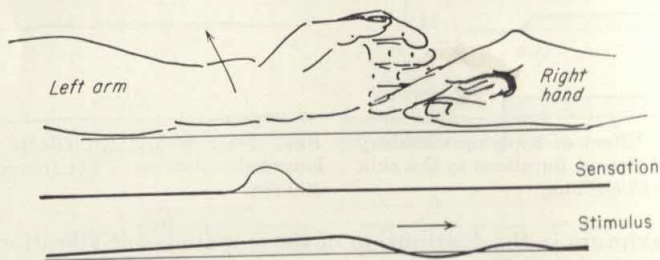


FIG. 13-33. Locus of the sensation with one arm and the other hand on the vibrating membrane.

But when the left arm was lifted the sensation immediately appeared under the right hand and seemed almost as strong as it had been before under the left arm. This is a surprising experience.

Another peculiarity of the inhibition along the skin of the arm is that on the membrane of the model the center of the sensation changed its position relative to the membrane when the amplitude was increased. Sometimes this shift was of the order of 2 cm for an amplitude change of 20 db, but sometimes it was as large as that shown in Fig. 13-34. Musicians have known for many centuries that the pitch of a tone in the lower part of the scale is lowered when the loudness is increased, and it

may well be that the shift observed in the skin model is a related phenomenon. One peculiarity of this shift is that in the extremities an increase in the intensity always produced a shift toward the head. This was true even when the direction of the traveling waves in the membrane was not toward the head, as shown in Fig. 13-34, but away from it.

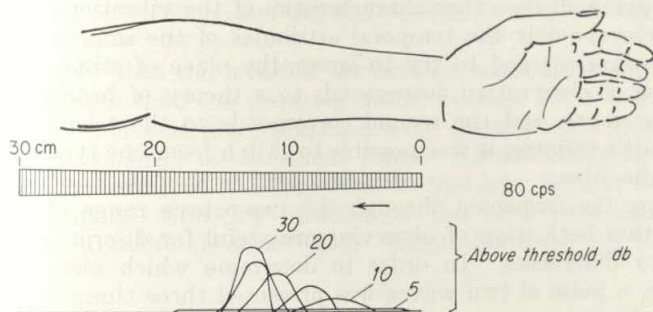


FIG. 13-34. Effect of stimulus intensity on the locus of the sensation.

A similar phenomenon is shown in Fig. 13-35. When the left arm was placed on the model with the hand close to the "stapes," the center of sensation for a given loudness was about 12.5 cm from the "stapes." If the right arm was then placed on the model in the opposite direction, the center of sensation for the same physical stimulus was about 6 cm from the "stapes." In both instances, the area of sensation seemed to

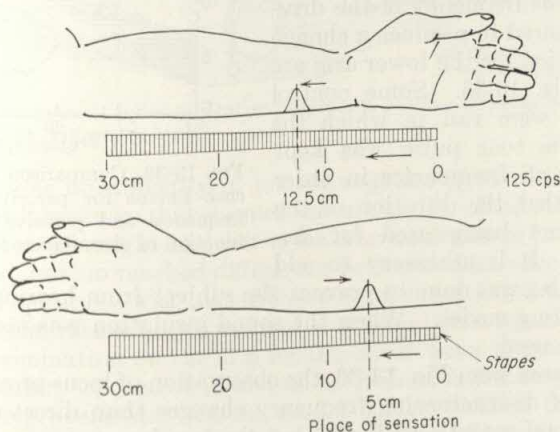


FIG. 13-35. Effects of orientation of the arm.

shift toward the head. The difference between the centers of sensation for the left and right arms increased as the amplitudes of the membrane were increased. It is therefore possible that for small intensities the center of sensation was localized at the same place on the membrane; and the difference between the centers of sensation for the two arm positions shown in Fig. 13-35 resulted from the fact that, for higher intensities, the sensation area shifted toward the head.

Observations of Place and Vibratory "Pitch" in the Model. When the model was set into vibration by a pulse of two or more waves or by a continuous tone, there were two ways in which a judgment could be made about the frequency of the vibration. One was to observe only the place of the pattern of stimulation along the membrane of the model and to ignore all the other characteristics of the vibrations; the second was to observe only the temporal attributes of the sensation produced by the vibrations and to try to ignore the place of stimulation. The first type of observation corresponds to a theory of hearing based on traveling waves, and the second corresponds to the telephone theory. With a little training, it was possible to switch from one type of observation to the other.

Varying the frequency through the two-octave range of the model showed that both ways of observing are useful for discriminating small frequency differences. In order to determine which method is more sensitive, a pulse of two waves was presented three times in rapid succession; the frequency was then changed and the three pulses presented again. The subject had to report whether he observed the change when he was concentrating on the place of the sensation or on the vibratory "pitch." The amplitude of the vibrations on the "stapes" was kept constant for both frequencies. The changes in the frequency of the driving unit required to produce a change in the sensation for the lower arm are shown in Fig. 13-36. Some control experiments were run in which the length of the tone pulse was kept constant for all frequencies in order to be sure that the duration of the pulse was not being used for discrimination. It is necessary to add that everything was done to prevent the subject from hearing the sound of the vibrating model. When the sound insulation was not sufficient, masking was used.

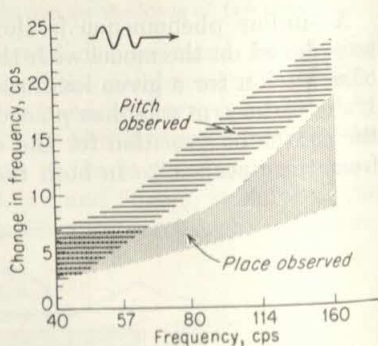


FIG. 13-36. Comparison of the difference limens for perceived vibration frequency and perceived locus as a function of stimulating frequency.

As can be seen from Fig. 13-36, the observation of locus proved to be an easier way of discriminating frequency changes than direct observation of the temporal sensations, for all but the low frequencies. One reason that the observation of place for the low frequencies is less accurate may be that the model is too short—only two octaves—and the reflection near the end cannot be effectively eliminated.

There was no need for training or learning to make a frequency discrimination by means of localization. When a subject placed his arm on the ridge of the membrane, he immediately felt the localization in its full definition.

To make the comparison even easier, the setup of Fig. 13-37 was used.

The ridge on the model was applied to one upper arm; to the other upper arm was applied a metal frame made of wires 3 mm in diameter and 3 cm long driven by an electric unit so that the phase and amplitude of vibration were constant along the whole length of wire touching the skin. The two systems could be driven simultaneously or alternately. The subject was asked which system was more useful for determining changes in frequency.

It was evident that the model of the cochlea contained more data on frequency changes than the vibrating frame, because in the model both temporal sensation and place sensation were present. For this reason the model was superior to the simple frame. In comparing the sensations in the two arms, it was surprising to find how difficult it was to memorize temporal vibratory qualities of the form presented which could be used to make absolute "pitch" determinations. On the other

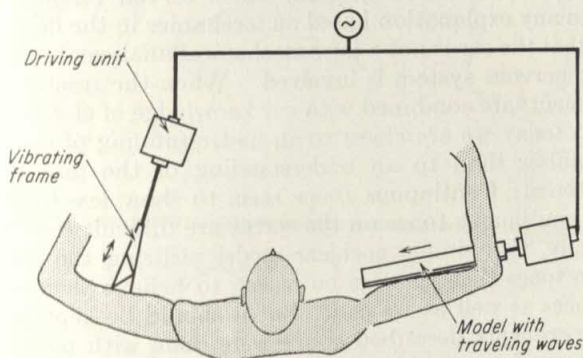


Fig. 13-37. Arrangement for comparative judgments of discrimination with the model and with a simple vibrating frame.

hand, there was no difficulty in memorizing the place of the sensation on the model because that seemed natural. To eliminate accidental differences between right and left arms, the positions of the arms were interchanged, but no marked differences between them were reported.

The next question was, can frequency discrimination be improved by some special means? No method was found that improved the frequency discrimination on the arm for the observation of temporal sensations. A variety of sizes and shapes of frames failed to produce any important improvements. In the model of the cochlea, the spread of the frequencies along the membrane depends on the variations in the stiffness along the membrane. In the experiments already reported, the stiffness in the model varied in accordance with the data of Fig. 13-22. There is no reason why the change in the stiffness per unit of length of membrane could not be decreased much further, thus decreasing the frequency range of the whole membrane from two octaves to one octave or even less. The largest frequency spread should be obtained when there is no variation at all in the stiffness of the membrane; for this reason a model was made with a constant membrane thickness. In

this way it was possible to produce an easily discriminated displacement of the sensory pattern of 8 cm on the lower arm when the driving frequency was changed from 60 to 61 cps. The whole frequency range, however, was proportionately narrow.

These experiments seem to show that there is in the cochlea a preliminary mechanical frequency analysis that produces along the basilar membrane a vibratory pattern with a flat maximum. This flat maximum is sharpened up by the nervous system, so that for a pure tone a distinct localization occurs. But a flat maximum is necessary in order that the nervous system can begin its inhibitory activity and thus sharpen the otherwise flat distribution of the stimulus. The whole analysis is completed in the course of one or two full cycles and is just as sharp as for a continuous tone. Wien's objection that an instantaneous frequency analysis is incompatible with sharp localization applies only to purely mechanical systems. This objection, which served for half a century as a threat to any explanation based on mechanics in the field of hearing, means only that the ear is not a pure mechanical analyzer but an analyzer in which the nervous system is involved. When the results of the foregoing experiments are combined with our knowledge of electrophysiology, it seems that today we are closer to an understanding of the analysis of short tone pulses than to an understanding of the discrimination of continuous tones. Continuous tones seem to show less inhibition, and responses to continuous tones on the cortex are difficult to record.

Anatomically, this simple cochlear model utilizing the skin works so well for pure tones that there is no reason to believe that birds cannot hear pure tones as well as we can. But it should be kept in mind that all of the experiments described above were done with pure tones only. For complex sounds or masking phenomena, the simple skin model shows a poor resolving power. The differences between the simple organ of hearing in birds and the complicated organ of Corti in mammals are not expected to show up in the hearing of pure tones but only in the hearing of more complex qualities. These more complex situations must be investigated to find out why and how the organ of Corti of mammals works. It is unfortunate that most experiments on birds are pure-tone experiments.

Differences between Perception by the Skin and by the Ear. A few remarks need to be made on the basic differences between the sensation on the skin and in the ear. In both fields, a large amount of research has been done, so that the basic data are readily available. The works on skin perception of Knudsen (2), Roberts, Skramlik, Katz, and Geldard are well known. Our problem is to determine what specific qualities the organ of Corti has that the skin does not have. Perhaps this knowledge will lead to an understanding of the special structure of the organ of Corti.

There are large differences in skin sensitivity on the various parts of the body, and to a certain degree it seems possible to extrapolate from that fact. For instance, it is well known that the skin on the arm is less sensitive than the skin on the thumb. To some extent, this difference

is a consequence of the fact that the area on the sensory cortex corresponding to a unit of surface on the thumb is much larger than that corresponding to a unit of surface on the arm. Penfield and Boldrey published a figure in which each section of sensory brain surface is related to a specific part of the body (see Fig. 13-38). The thumb occupies about as large a surface as the whole arm. To complete the figure for

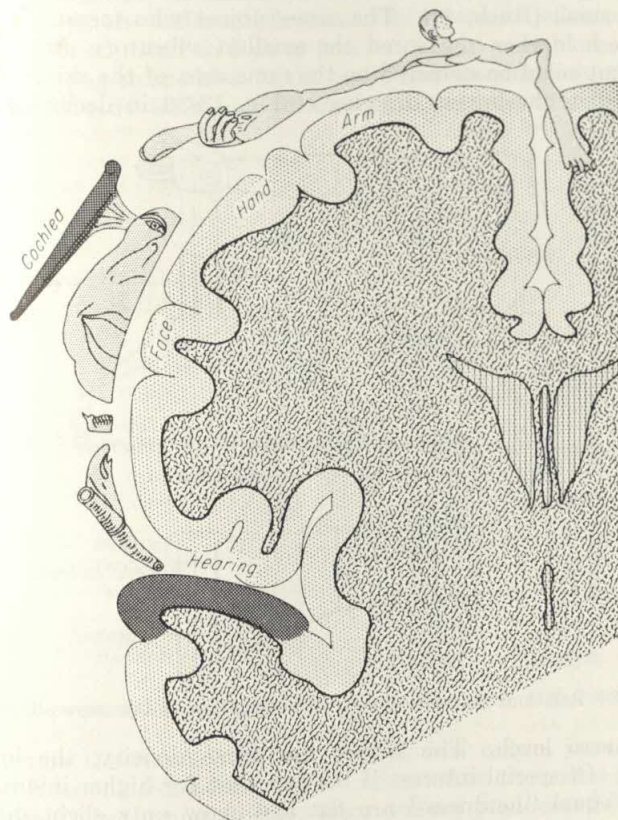


FIG. 13-38. Comparison of the sensory areas of the brain supplying the arm and the cochlea.

present purposes, the cochlea was unrolled and its size made to correspond with the area of hearing; the cochlea was then affixed to the face. Although this type of representation is not to be considered precise, it still makes it clear that the nerves in the cochlea occupy an area on the cortex comparable to the area occupied by the skin surface of the whole face. Because the corresponding area of the cochlea on the brain is still relatively larger than the corresponding area of the thumb, the changes in sensory perception from the arm to the thumb had to be extrapolated in the same direction in order to arrive at the properties of the cochlea.

How some of the qualities change along the line from the thumb to the upper arm are shown in Fig. 13-39. The uppermost drawing shows a factor obtained by dividing a certain surface of the cortex by the corresponding surface on the skin. The nerve density on the thumb is high relative to that on the arm. Because of the higher nerve density on the thumb, the two-point threshold (that is, the smallest distance between two needle points that can be discriminated on the skin surface) is relatively small (Ruch, 1). The same subject who measured the two-point threshold then measured the smallest vibratory amplitudes for 100 cps that could be detected on the same area of the skin. They are represented in the lowest drawing of Fig. 13-39 in decibels below an

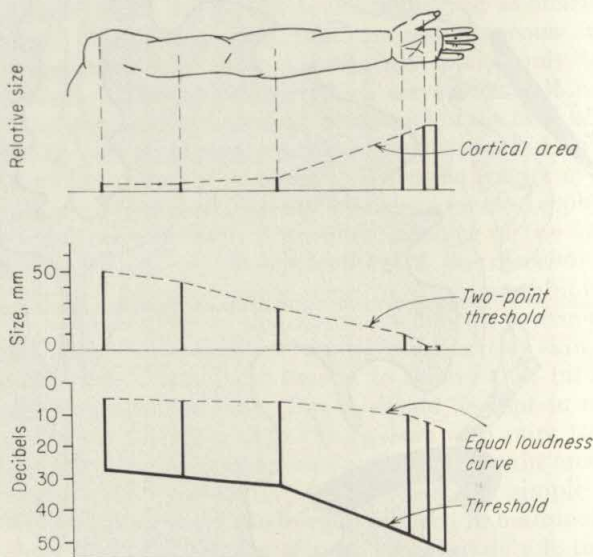


FIG. 13-39. Relations between density of innervation and sensory phenomena.

arbitrary zero level. The higher the nerve density, the lower the threshold. Of special interest is the fact that for higher intensities the curves of equal "loudness" are flat and show only slight differences between various points on the fingers and arm. For points of the skin of low nerve density, therefore, the intensity increases much more rapidly than for points of high density. In the language of otology, we should say that skin spots with low nerve density show recruitment.

On the thumb the whole stimulus range between threshold and pain is about 40 db, but in the ear it is about 120 db for a 1000-cps tone, which means that the cochlea must have a very low two-point threshold. Comparisons of this type indicate the direction in which we must look for the differences between the skin and the ear.

To discover more details of the differences between the ear and the skin, the conditions of stereophonic hearing had also to be reproduced. The equipment is seen in Fig. 13-40. Two microphones picked up the

sound from a certain direction and produced corresponding vibrations in two identical models of the cochlea that were pressed against the inner surface of the lower arm. Since the driving unit was at the top, the lower frequencies were located below, and the higher frequencies were located above.

Sensations of direction occurred as a combined effect of magnitude and time differences. Because the magnitude increased rapidly on the skin of the arm, the difference between the intensity levels on the two sides had to be adjusted to 1 db or less.

It is interesting to see how, in the world of skin sensation, an external space was gradually built up. In the beginning, the sound source was

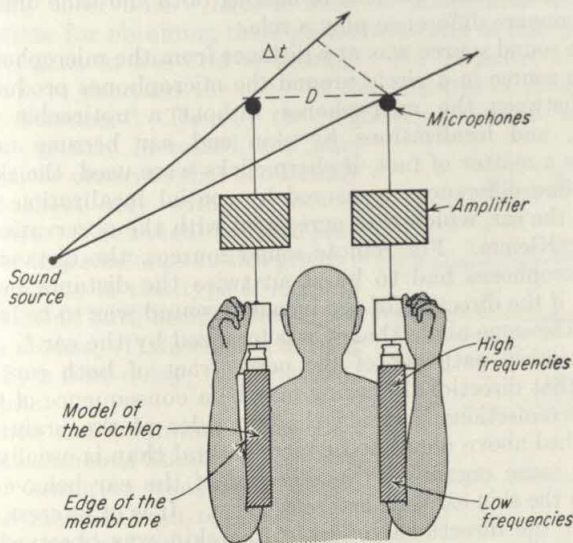


FIG. 13-40. Arrangement for stimulating both arms, in analogy with binaural hearing.

moved within the room, and there was at first only a jumping of the sensation from one side to the other. Even when the sound source was symmetrical to both microphones, there was no pronounced localization intermediate between the two models of the cochlea. But in time this situation changed, and the sound source seemed to move continuously in a line from one model to the other. When the distance from the sound source was increased, no change in the position of the skin localization was felt. The magnitude of vibration simply decreased and faded out on the same spot. The skin perception was one-dimensional.

When the experiment was repeated with the subject watching the movements of the sound source, the subject at some point experienced a sensation of distance; and after a time every change in magnitude, produced either by changing the distance between the sound source and the microphone or simply by decreasing the input to the sound source, produced a sensation of distance, and the field of perception on the skin

became two-dimensional. By means of a switch, the two microphones could be connected to both ears to facilitate comparison of the differences in localization by the ear and by the skin.

When the sound source was close to the microphones, sound localization by the ear and by the skin were very different. This difference results from the fact that on the skin the magnitude increases much more quickly than it does in the ear. The skin reacts primarily to sound-pressure differences between the two microphones. On the skin, localization is determined almost completely by the changes in sound pressure on the two microphones during movement of the source, and the time difference between the arrival of the sound on the two microphones is unimportant, whereas in hearing both the time difference and the sound-pressure difference play a role.

When the sound source was at a distance from the microphones, movement of the source in a circle around the microphones produced a time difference between the microphones without a noticeable change in magnitudes, and localizations by skin and ear became much more similar. As a matter of fact, if sharp clicks were used, the skin's sensitivity for time differences measured by spatial localization was about half that of the ear, which is in agreement with the observations already reported by Klemm. For remote sound sources, the distance between the two microphones had to be about twice the distance between the ears in man if the direction of the incoming sound was to be localized by the skin at the same angle that it was localized by the ear.*

The anatomical pathway of the nerve tract of both ears gives the impression that directional hearing may be a consequence of the special neural interconnections between the two sides of the brain. But the effect described above seems to be more general than is usually assumed, because the sense organs of the skin and of the ear behave similarly, even though the skin exhibits less sensitivity. It is of interest, therefore, to note that the directional effect of the skin was observed not only when the stimuli of both microphones were applied to symmetrical points on both sides of the body, but also when the stimuli were applied to points close together on the same side. Even the definition of the effect was the same in both cases. Therefore this type of interaction effect between two stimuli is common to all surface areas of the skin, and the minimum time differences necessary to suppress one of the stimuli are about the same at all points on the surface of the human skin.

SENSATIONS ON THE SKIN SIMILAR TO AUDITORY PHENOMENA†

A mechanical dimensional model of the cochlea has just been described which exhibited vibrations along its length similar to the vibrations of the basilar membrane in the inner ear. The sensory cells of the organ of Corti were represented in the model by the skin of the arm, and the

* [This statement is corrected in the next article, p. 573. When subjects are well trained they give similar lateralizations for both ear and skin.]

† Article 79 as listed in the Author's Bibliography. Published in 1957.

sensations on the skin resulting from vibratory stimulation were compared with the hearing of tones. As the skin has somewhat different sense organs from the organ of Corti, it is of interest to find out what phenomena in hearing can be duplicated on the model and what phenomena are obtainable only in the ear. From such observations it should be possible to discover which phenomena are bound to the special nervous system of the organ of Corti. This approach may bring a closer understanding of the functioning of the organ of Corti.

The model, together with the skin of the arm used as a receptor, has a second use. With the model it is possible to improve on some of the special properties of the organ of Corti so that certain phenomena are more readily observable. Thus it may be possible to determine the best conditions for obtaining these phenomena and in this way to facilitate observations in the field of hearing. For instance, on the model it is possible to decrease the slope of the changes in elasticity of the "basilar membrane." Thereby the frequency resolution of the model ear may be greatly increased, and phenomena may be observed that auditorially can be obtained only with the utmost concentration. The much-discussed phenomenon of beats belongs to this group.

As a beginning in this type of research three phenomena have been studied in the ear and in models, (1) directional hearing produced by a time delay, (2) harmonics, and (3) beats.

Summation and Inhibition on the Skin for Two Simultaneous Stimuli. The great variety of sensation that the nervous system can mediate with only a few elements is due to the fact that two similar stimuli may add to or diminish each other's effect, or may not interact at all, depending sometimes on small changes in circumstances. In many ordinary situations the nervous system works almost like a linear system, and its only effect is on the size of the sensation. But there are some critical situations in which a small change in the stimulus may alter the whole aspect of the sensation.

This sensory situation can be demonstrated by a simple experiment. The tips of a pair of compasses were pressed against some area of skin, and the distance between the tips was varied. In the experiment shown in Fig. 13-41, the inner surface of the forearm was used, and the tips each had a diameter of 1 mm. The distance between them is given at the left of the figure. In the drawings the horizontal lines indicate the surface of the skin, and the curve represents the magnitude and spread of the pressure sensation produced by the tips of the compasses. As the distance

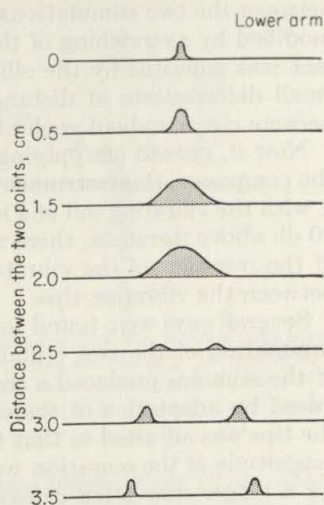


FIG. 13-41. Summation and inhibition in stimulation of the skin by simple pressure at two points at varying distances.

between the tips increased, the magnitude and spread of the sensation increased also. But as the distance exceeded 2 cm, the tips suddenly were perceived separately, and they seemed weak and closer to each other than the physical distance between them. This change was due to a reciprocal inhibition of the two separate stimuli. With a further increase in the distance between the tips, the magnitude of the pressure sensation increased until at 3 cm they were almost independent of each other, and the magnitude of each was as large as when only one tip of the compasses was pressed against the skin.

The same results were found on other parts of the skin. Inhibition was especially easy to observe on the heel of the thumb, where there are no hair follicles, and consequently a pressure sensation there did not show the local increase often found when the tip of the compasses was accidentally pressed directly on the root of a hair. Because of the hair follicles, it was found best to provide the compasses with ball tips about 3 mm in diameter. It is obvious that for small distances the interaction between the two stimulations produced by the impression on the skin is modified by a stretching of the skin between the two impressions. This fact was indicated by the elliptical shape of the impression, but for the small deformations at distances of 1 cm or more the skin deformation became circular about each of the tips.

Now if, instead of applying the slow pressure produced by the tips of the compasses, this instrument was made to vibrate at 50 cps by touching it with the vibrating coil of a loudspeaker unit with a vibratory amplitude 20 db above threshold, there was no change in the pattern of distribution of the intensity of the vibratory sensation as a function of the distance between the vibrating tips.

Several ways were found for altering the critical distance at which the summation of the two stimuli changed into inhibition. The intensity of the stimulus produced a small variation. Larger variations were produced by adaptation of the cutaneous nerves. If the distance between the tips was adjusted so that the two stimuli were felt separately and the magnitude of the sensation was small, then keeping the stimuli constant for a longer time often caused the inhibition to change into summation and the magnitude of the sensation to increase. When only one tip was pressed against the skin, however, adaptation decreased the magnitude of the sensation.

The inhibition was suppressed to an even greater degree if, instead of applying the static pressure or the 50-cps vibrations, the compasses were connected to an electrodynamic driving unit actuated by short condenser discharges. When these sharp clicks were applied to the skin by the tips of the compasses, all subjects reported only summation for all the distances shown in Fig. 13-41.

This observation suggests that the neural pathways in the skin may be entirely different for a long-lasting a-c stimulus and a single short click. Single short simultaneous clicks probably set in action the direct lines to the higher levels of the nervous system, without being inhibited by lateral connections whose firings come too late. This observation

brings to mind the fact that the effects of clicks are easy to observe in the auditory cortex, but the effects of pure tones are difficult to detect with present methods. It is suggested that even if we succeed in tracing the neural path of a click from the cochlea to the cortex, we shall still not be sure that a pure tone will follow this same route.

Interaction between Two Stimuli with a Time Delay. When there is a time delay between two stimuli, inhibition plays an important role. For example, the well-known phenomenon of directional hearing can be duplicated on the skin (Katz). For a closer investigation of this phenomenon, two tips attached to two electromagnetic driving units were placed on

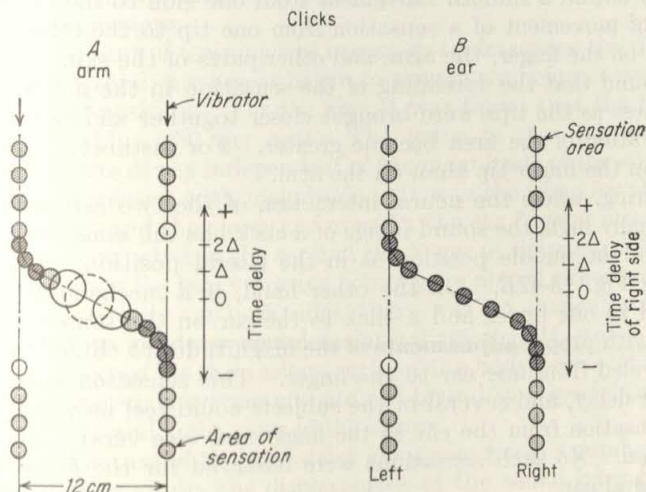


FIG. 13-42. The inhibition of one click by another as a function of their temporal interval. (A) represents the stimulation of two points on the skin 12 mm apart, and (B) represents stimulation of the two ears. The time scale runs vertically, with positive values signifying priority for the left stimulus. The shading of the circles represents sensory intensity.

both sides of the end of the thumb, or on two points about 12 cm apart on the inner side of the arm. A timing device was used to discharge two condensers through the driving units with a certain time delay as represented on the right side of Fig. 13-42A. When the vibrator on the left side of this figure received its current earlier than the driver on the right side, for larger time differences two discrete, sharp pulses were felt on the skin, one on the left side followed by one on the right. The intensity of the two pulses was about the same.

As the time delay was made smaller, however, the sensory intensity on the right side decreased as indicated in Fig. 13-42A by an unshaded circle, whereas the intensity on the left side increased until the effect on the right side was completely suppressed and the whole thrust produced by the side was felt only on the left side. The spread of the sensation of pulses was felt only on the left side. The spread of the sensation of vibration along the surface of the skin is represented schematically by the size of the circle, and the intensity by the degree of shading. As

the time delay approached zero, the area of the sensation moved to a position halfway between the two tips, its size increased, and its intensity decreased. As the sign of the time delay became negative, the pattern was repeated on the other side, as can be seen in the figure. The sensory area became smaller and more dense and then lost its intensity. If a small tip was used on one side while the surface of the other vibrator was made ten times larger, the phenomenon of traveling from one side to the other did not change, but the sensory area was greater under the larger tip, and still greater when the sensation was in the middle.

It was important in these observations that the two clicks be equally strong to obtain a smooth movement from one side to the other. This pattern of movement of a sensation from one tip to the other has been obtained on the finger, the arm, and other parts of the skin. In general it was found that the spreading of the sensation in the middle position became less as the tips were brought closer together and as the density of innervation of the area became greater. For instance, the area was smaller on the finger tip than on the arm.

In hearing, where the neural interaction of the two ears seems to be exceptionally high, the sound image of a click has the same intensity and density in the middle position as in the lateral position. This fact is shown in Fig. 13-42*B*. On the other hand, if a mechanical pulse was presented to one finger and a click to the ear on the same side, it was possible with proper adjustments of the magnitudes to obtain a sensation that traveled from one ear to the finger. This sensation was weak for zero time delay, and several of the subjects could feel only the jumping of the sensation from the ear to the finger and vice versa, with nothing in between. No such sensations were observed for the finger and the contralateral ear.

It should be pointed out that some subjects did not always succeed in fusing the sensations on different parts of the skin. Fatigue or excitement may be the reason, or some personal characteristic. The problem is almost the same as with fusion in stereoscopic vision. During actual shooting, in the war, it was surprising how flat the field sometimes looked through binoculars, even with a large base.

To find out whether or not this lateralization depends on the condition of the end organs, condenser discharges were used for direct stimulation of the same points on the skin to which the vibrators were applied. The pattern of displacement and intensity was exactly the same as in Fig. 13-42*A* for the same delay times. Then the skin was anesthetized with ethyl chloride spray, and again, with proper adjustment of the intensity of the single stimulus, it was possible to obtain exactly the same pattern as Fig. 13-42*A*.

The above-mentioned experiment suggests that the lateralization occurs at a higher level of the nervous system, and so it seemed worthwhile to try to localize simultaneously a click heard by the ears and a pulse felt on the skin. For this purpose two earphones were connected to the input of the electrodynamic drivers. The sound image of the clicks and the pulse on the skin could both be felt, moving separately

from side to side. When the two earphones were then exchanged, however, the same time delay simultaneously moved the sound to one side and the pulse to the other side. Certainly the auditory and skin sensations did not mask one another.

A close study of Fig. 13-42 shows that, as the delay time increases, the sensory area moves to the lateral position in two stages. When the delay time reaches a certain value Δ , the lateral movements slow down. Then when the time has been increased to 2Δ , the extreme lateral position is obtained, and shortly afterward the sensory area begins to split apart. This behavior holds for the sense of vibration, for hearing (page 278), and for electrical stimulation as well. Inhibition is evidently achieved in two successive steps.

A certain amount of training was necessary to determine the time delay for which the lateral movement began to slow down before it reached the extreme lateral position. For the skin it was found that the two steps were equal within ± 30 per cent. The value of $\Delta = 1.2 \times 10^{-3}$ sec. For some subjects Δ was independent of the magnitude of the stimuli, but for others it increased with magnitude. It was the same for the finger, the arm, the leg, and the chest, and even for the ear,* and it was the same for lateralizations between the ear and the finger of the same side. Even on the chest, when the two vibrating points were placed either both on one side or symmetrically on both sides, there was no change in the delay time required to produce complete lateralization. It seems that the inhibitions observed on the various parts of the body represent a general feature of the nervous system and are not bound to a special interaction between the left and right sides of the cortex.

The general nature of the time delay constants raises a number of questions. In human adults the displacement of the sound image from the middle to the side is achieved by the same time delay between the ears as when an actual sound source moves around the head. Accordingly, estimates made of the position of a sound image coincide with the direction of an actual sound source. In a child, however, the distance between the two ears is smaller, and Δ has to be smaller too if the time delay between the two ears is to be used for sound localization. This brings up the question of the maturation of the nervous system. In vision it is known that if a person wears a reversing prism, his movements at first are all opposite to the correct direction, but after about 2 weeks he will have adjusted to the reversal and will make correct movements (I.

* On p. 568 the time delay for extreme lateralization on the skin was given as about twice that required for lateralization in hearing. At that time it was not clear that for the skin as well as for the ear the lateralization occurs in two steps, and the extreme lateral position takes about twice as much time as displacement to the point where large movements of the sensation are no longer present. On the enlarged model of the cochlea, with the arm placed along the edge of two long vibrators, the subject found the extreme lateralization, when the stimulus was felt directly on the surface of the skin, for a time delay of 2Δ . For sound localization, however, the subjects thought that they had extreme lateralization for a delay of Δ . If the attention of the subjects was not specifically called to this point, they all gave 2Δ for the skin and Δ for the ear.

Kohler). When the prisms are removed, it will again take 2 weeks for the person to return to normal. Such a high degree of adaptation does not occur in lower animals. For instance, if the eyes of a frog are rotated 180° by an operation, he will jump after a fly in the wrong direction to the end of his life. There does not seem to be any adaptation at the lower levels. Since the directional hearing of chickens is about as good as man's, either Δ must be very small for the nervous system of the chicken, or the chicken's directional hearing must be based on something other than the time delay between the ears. These problems, though interesting, will not be discussed further at this point.

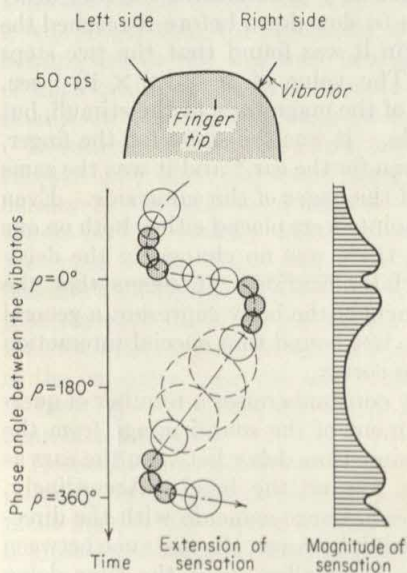


FIG. 13-43. Interaction of two sinusoidal vibrations of equal amplitude as a function of their phase relation.

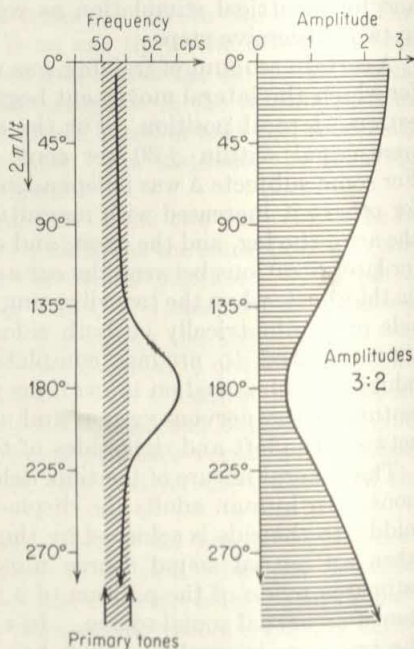


FIG. 13-44. Frequency and amplitude changes during the beat cycle for two beating tones with an amplitude ratio of 3:2, according to calculations by Helmholtz.

To investigate further the similarity between the skin sensations and hearing, an analog of the rotating tone (a tone revolving around the vertical axis of the head) was produced on the tip of the finger. For this purpose the tip of a vibrating unit with a frequency of 50 cps was placed on one side of the finger and on the other side a unit vibrating at 50.2 cps, as illustrated at the top of Fig. 13-43. When the intensities of both sides were made equal, the sensory area moved periodically from one side of the finger to the other, just as for the rotating tone. The time axis in Fig. 13-43 runs from the top downward, and also, as in Fig. 13-42, the diameters of the circles indicate the apparent spread of the sensory area,

and the degree of shading indicates the density or intensity of the sensation. When the phase angle between the two vibrators was zero, the magnitude decreased a little, but in going through 180° of phase there was a substantial decrease in magnitude, and almost the whole finger seemed to vibrate. Localization was sharpest in the extreme lateral position at either side. But just as for the ear, clicks were much better localized than simple vibrations.

Beats. A few decades ago the hearing of beats was much discussed, though no final agreement was reached concerning the observed phenomena. Of special interest was the question whether changes of pitch occur in a beating tone. Helmholtz (1) calculated the variation in frequency of the intertone for two beating tones of unequal amplitudes. Figure 13-44 shows the variation in frequency (on the left) and the amplitude (on the right) during one cycle of beats for two beating tones whose frequencies were 51 and 50 cps, respectively, and for which the amplitude of the higher tone was 1.5 times that of the lower tone. As can be seen, at maximal amplitudes the frequency of the intertone is a little more than halfway between the two beating frequencies. But for minimum amplitude the frequency of the intertone moves far above the frequency of the higher primary tone. Helmholtz said that he could hear these changes of frequency, but Stumpf (1,2) was unable to do so. The whole question of beats was summarized by Wever (1).

In order for the changes in pitch to be observable during beats, one beat has to last at least 1 sec. The maximal frequency change during one cycle of beat is given by the formula $N = n(2AB)/(A^2 - B^2)$; $A > B$, in which n represents the number of beats per second, A the amplitude of the tone with the higher frequency, and B the amplitude of the lower tone. For the amplitude ratio given above, this formula gives a maximal frequency change of 2.4 cps. Unfortunately the just-perceptible frequency change at a convenient loudness level for a 50-cps tone is about 2 cps and for a 500-cps tone is about 3 cps for uniaural observation. Hence it is difficult to hear variations of pitch during beats.

In an earlier section an enlarged model of the human cochlea was described in which the movements of the basilar membrane could be duplicated on a large scale. When the forearm was placed on this model, stimulation with a tone produced a sensation on a restricted area of skin (1 to 2 cm wide), and this area moved along the surface of the arm in accordance with changes in the frequency of the tone. This model was used to investigate some of the similarities between hearing and the sensations of the skin. With beats the model presented the same difficulties as the ear. When the beat frequency was one per second, the displacement of the sensation on the skin was too small for the subject to be sure about the feeling of an intertone. But with the model it was not difficult to increase the frequency resolution. By changing the elastic properties of its membrane, it was possible to obtain a displacement of the sensory area of almost 10 cm along the surface of the skin for a frequency change of 1 cps. It then was easy to follow the sensations during the beats. Their course is shown in Fig. 13-45. On the left side the physical stimulus

is shown, and on the right side the distribution of the sensation along the surface of the arm. The high frequencies gave a stimulation of the skin

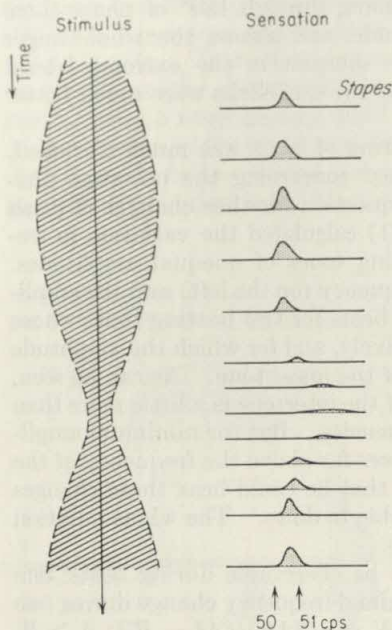


FIG. 13-45. Changes in the locus of the vibratory sensation on the arm as observed in the cochlear model. The vibratory amplitude during the beat cycle for two frequencies of 50 and 51 cps is shown on the left, and successive locations of the sensation along the arm are shown on the right.

exactly as described by Stumpf for hearing.

After observations of the different phenomena on the model it was surprising to find the degree of similarity to the ear. With two tones properly adjusted for magnitude and beat frequency, it was possible with training to observe a just-perceptible change in "pitch" during the period of amplitude increase. This observation confirms that of Helmholtz. If the amplitudes of the two tones were equal, then there was no variation in "pitch," and this is in agreement with the calculations and observations of Taylor. During all these experiments on the variation of "pitch" during beats the subjects had the impression that the sensation of beating was described by the displacement of the sensation along the arm, and that the vibration as such did not play any part in the phenomenon.

As the beat frequency is increased further, a limit is approached in hearing where the two tones separate and are recognized as such. Here is a difference between the ear and the model, for the model lacks something that operates in the cochlea so as to reduce the interaction between

to the right along the horizontal lines, and low frequencies to the left. When the amplitude was at its minimum there was sometimes no sensation, for the amplitude was below threshold. As the amplitude increased, the "pitch" became lower, and at the same time the sensation was sharpened. The "pitch" change of the intertone could easily be observed. But it becomes evident, too, that the maximal amplitudes produced a fatigue or adaptation effect, so that the movements of the sensory area were not as easily observed during a decrease of amplitude as during an increase. To demonstrate this difference, the tones were automatically switched off during the maximum, which facilitated the observation of the "pitch" variation.

If the beat frequency was increased, the sensation at maximal amplitude did not decay rapidly enough and masked the weaker "pitch" change (which lasted only a short time) at the minimum. The only sensation then was a pulsation with constant "pitch,"

tones that are well separated along the frequency scale, as shown in masking.

In this connection, it should also be mentioned that with the model no subject had a sensation of consonance for frequencies such as 70 and 140 cps when presented consecutively, whereas this sensation is striking when these two tones are heard.

Harmonics on the Skin. In recent years the hearing of beats has again received attention because of the use of the method of best beats to determine the harmonics produced in the ear by a pure tone. In this method a pure tone with a frequency slightly different from that of one of the harmonics is superimposed upon the fundamental, and the amplitude of the superimposed tone is varied until the beats heard are maximal. It is then assumed that the amplitude of the superimposed tone is equal to the amplitude of the harmonic produced by the fundamental. This method has been used by a number of experimenters.* All these observations lead to the conclusion that the aural harmonics are large; thus the amplitude of the second harmonic (whose frequency is twice that of the fundamental) turns out to be more than 30 per cent of the amplitude of the fundamental. The question is, do these large distortions have a physical existence, and in what part of the ear do they arise?

It has been shown that the eardrum produces nonlinear distortions only for sound pressures above the threshold of feeling (page 332). The same holds for the movements of the basilar membrane when only the periodic movements are taken into account (page 464). Eddies may produce a displacement of the zero position of the basilar membrane, but this does not affect the periodic movements because this displacement is built up only during several periods by mass forces of the fluid. The organ of Corti might have inside it a nonlinear mechanical distortion, but this would not modify the vibrations of the basilar membrane, for it is known that it is possible even to brush the organ off the basilar membrane without producing any notable change in the vibratory pattern of the membrane (page 467).

At the moment there is no proof that the organ of Corti produces harmonics, in spite of evidence that the shearing forces inside the organ of Corti may do so. When the electrical response of the cochlea is recorded, large harmonics are observed (Stevens and Newman; Wever, Bray, and Lawrence, 1). It may be that these distortions are produced by a combination of the microphonics plus the action potentials of the nerves, since even with differential electrodes it is difficult to separate these two phenomena. In addition, polarization effects on the cell walls may play a role. Chocholle and Legoux (see Legoux, Chocholle, and Wisner) suggested that the nonlinear distortion of the microphonics may have several causes.

With these circumstances in mind an investigation was made of the harmonics produced on the skin by use of the method of best beats just as for the ear. The skin has no organ of Corti, and the mechanical

* Wegel and Lane, Fletcher (3), Békésy (p. 332), Moe, Lewis, Opheim and Flotorp, Lawrence and Yantis.

forces are transmitted through a single layer to the sense organ, instead of along the complicated path through the middle ear and the perilymph. Large amplitudes were produced with an electrodynamically driven vibrator and were measured with a condenser microphone (Backhaus, 1). For most measurements the tip of the finger was used, mainly because it provides a wider range of intensity. In most of these measurements the movements of the vibrator were tangential to the surface of the skin, so that the vibrations did not penetrate into the deeper layers. The use of pure shearing forces made the measurements easier to reproduce, but in general the result was no different if the tip of the vibrator was simply pressed against the tip of the finger.

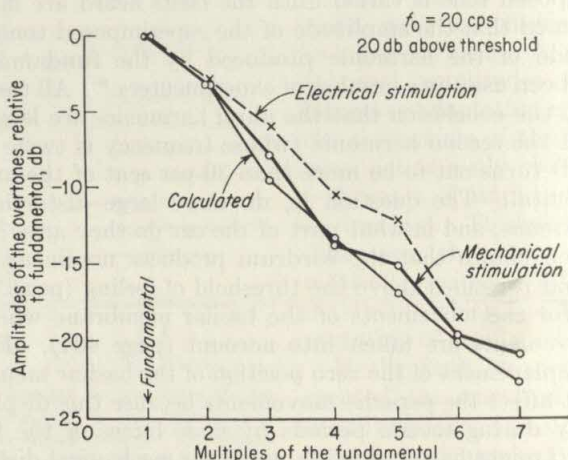


FIG. 13-46. Observations of best beats as observed on the finger tip. The fundamental (first harmonic) was 20 cps, at a level of 20 db above threshold.

There are several ways to observe best beats. One is to concentrate on the maximum of the "loudness," or the minimum, and adjust the amplitude of the superimposed tone so that the two become distinct. An effort was made to adjust the superimposed tone so that the variation in "loudness" was maximal during the beats. The heavy solid line in Fig. 13-46 represents the amplitudes of the superimposed vibrations relative to the amplitude of the fundamental vibration of 20 cps for mechanical lateral stimulation of the finger tip. (The thin lines of this figure will be discussed later.) For the higher harmonics, the vibratory amplitude that gave the best beats decreased rapidly. But as it turned out, the magnitude of the harmonics was larger on the skin than in the ear. The amplitude of the second harmonic* on the skin was 70 per cent of the fundamental. About the same value was obtained on the other areas of the skin that were less sensitive than the finger tip. In comparing the amplitude of best beats on different sensitive spots of the skin

* It should be borne in mind that the second harmonic is the first overtone, the third harmonic the second overtone, and so on.

the findings of Egan and Klumpp were borne in mind. They showed that near threshold there is a tendency to overestimate the amplitude of the best beats because the best amplitude is not approached from the lower as well as from the higher amplitude. An attempt was made to avoid this mistake as much as possible.

The large values obtained for the harmonics raised the question whether the method of best beats really measures the harmonics. The method of best beats has been used by musicians for hundreds of years to select a single component from a complex sound. It was natural,

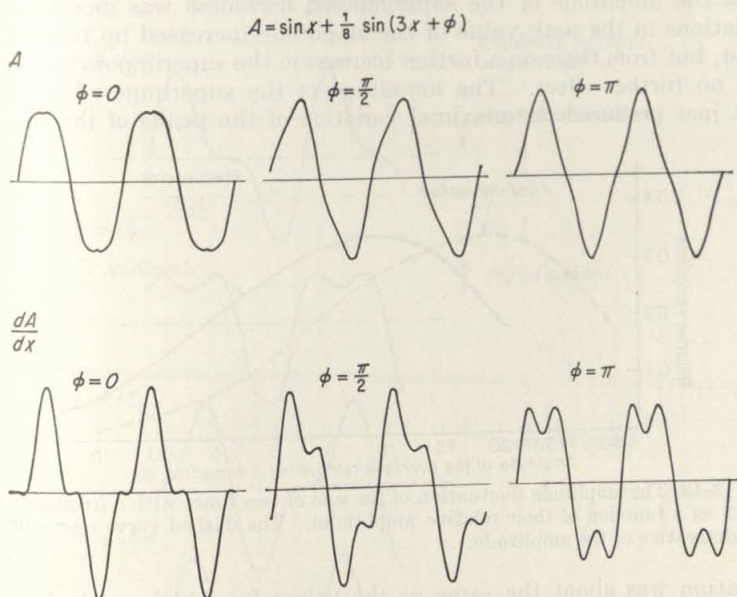


FIG. 13-47. Wave patterns of the sum of two tones with a frequency ratio of 1:3. Above are amplitude curves, and below are the first derivatives of these curves for three phase relations.

therefore, to use the same method to pick out harmonics after the concept of nonlinear distortion became familiar in telephone engineering. But let us assume for a moment that there is no nonlinear distortion at all and investigate what sensation we should expect to be produced by a sinusoidal vibration superimposed upon a stronger fundamental vibration. Let us first consider an odd frequency ratio like 1:3. In Fig. 13-47 the upper row of drawings shows the amplitude for three different phase relations, and the lower row of drawings the variation of the amplitude with time. During a beat all the different phase relations follow each other successively. As can be seen from the drawings, the variation in phase produces two different changes: (1) the maximal amplitude of the complex vibration varies periodically, and (2) there is a change in the slope at which the amplitude rises with time. The question is, which of these two changes produces the sensation of beats? In an effort to

find this out, the vibrations of the vibrator were picked up by a condenser microphone and displayed on an oscilloscope together with the first derivative, while at the same time the vibrations were observed with the finger tip. It came out clearly that the magnitude was maximal when the shape of the complex tone was triangular ($\phi = \pi$) and when the amplitude reached its peak value during the beat. The minimum magnitude corresponded to the pattern with the flat top ($\phi = 0$). From this it appears that the beating sensation results from the variation in the peak value of the amplitude during the beat cycle.

As the amplitude of the superimposed harmonic was increased, the variations in the peak value of the amplitude increased up to a certain point, but from there on a further increase in the superimposed harmonic had no further effect. The amplitude of the superimposed harmonic that just produced the maximal variation of the peaks of the complex

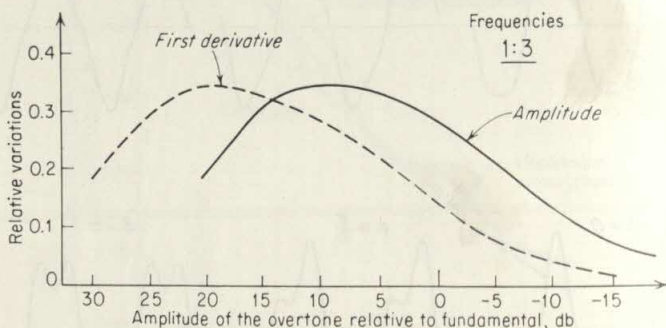


FIG. 13-48. The amplitude fluctuation of the sum of two tones with a frequency ratio of 1:3 as a function of their relative amplitudes. The dashed curve represents the first derivative of the amplitude.

vibration was about the same as the values for which most observers obtained the best beats. Increasing further the amplitude of the superimposed vibration did not increase the magnitude of the beating sensation, for the variation of the peak values remained constant, and only the absolute value of the vibratory amplitude increased. On the contrary, the sensation of beating decreased because magnitude variations were about proportional to the percentage changes in amplitude. Figure 13-48 shows relative variations of the peak values of the amplitude during the beats (*i.e.*, peak amplitudes divided by the mean peak amplitude) as a function of the amplitude of the third harmonic relative to the amplitude of the fundamental. There is a maximum when the amplitude of the third harmonic is 9.5 db below the amplitude of the fundamental. As can be seen in Fig. 13-46, the subjects obtained amplitudes slightly larger than this for the best beats of the second harmonic.

The dashed curve in Fig. 13-48 represents the relative variation in peak values for the steepness of the vibratory pattern. The maximum of this curve is at a much lower amplitude of the superimposed harmonic than those found in the experiments.

For the even-numbered harmonics the situation is similar. Figure 13-49 shows vibratory patterns of a 1:2 frequency ratio for different phase relations. The patterns of the even-numbered harmonics are asymmetrical with the time axis, whereas the odd ratios are symmetrical. A d-c pressure superimposed upon the complex vibrations with an odd number of harmonics did not influence the beating sensation, in contrast with the complex vibrations obtained with an even number of harmonics. For a phase $\phi = \pi/2$ in Fig. 13-49, the downward movement of the

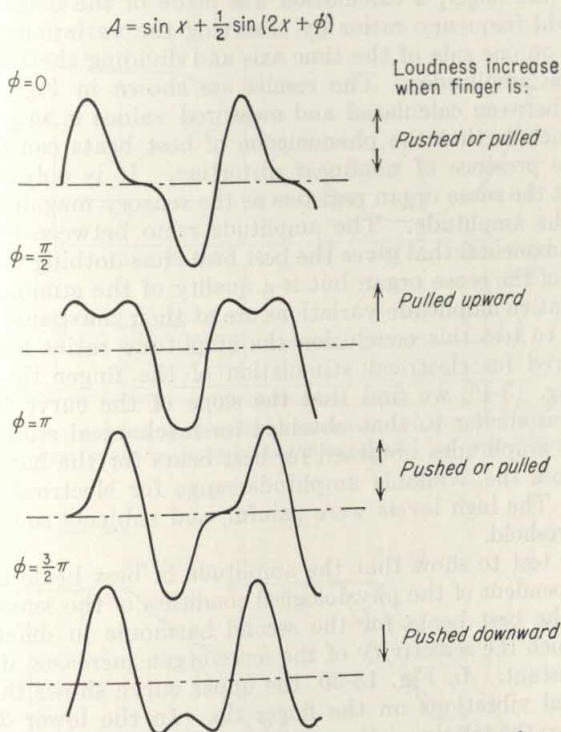


FIG. 13-49. Wave patterns for the sum of the fundamental and second harmonic with different phase relations. On the right are indicated the displacements of the finger that will produce noticeable increases in intensity with these wave patterns.

vibrator was larger than the upward one, and therefore the peak of the downward movement determined the magnitude level. The relative downward movement of the vibration on the finger tip could be increased by raising the finger, and in this manner the magnitude could be increased. When the phase was $\phi = 3\pi/2$, a downward movement of the finger produced an increase in the magnitude. These magnitude increases produced by a pre-tensing of the skin were large. When the vibratory pattern was symmetrical with the time axis, as for $\phi = 0$, an up or down movement of the finger tip produced a small increase in magnitude compared with the indifferent state. The indifferent state could be pro-

duced by a slight push or pull on the skin, and this made the sensation symmetrical. This symmetrical sensation lasted for only a few seconds. It should be mentioned in this connection that the "pitch" of the vibratory sensation changed whenever the stimulating peak of the amplitude was made, as in the upper drawing of Fig. 13-47 for $\phi = 0$, or in Fig. 13-49 ($\phi = \pi/2$), where the addition of a d-c displacement to the finger caused the flat peak of the amplitude to become the stimulating one.

Since a small positive or negative displacement is always present in the skin of the finger, a calculation was made of the magnitude of the beats for odd frequency ratios by observing the variations of the peak amplitudes on one side of the time axis and dividing them by the mean value of the amplitudes. The results are shown in Fig. 13-46. The agreement between calculated and measured values is so good that we have to conclude that the phenomenon of best beats can be explained without the presence of nonlinear distortion. It is only necessary to assume that the sense organ registers as the sensory magnitude the peak values of the amplitude. The amplitude ratio between the harmonic and the fundamental that gives the best beats has nothing to do with the physiology of the sense organ but is a quality of the stimulus signifying that the relative amplitude variations are at their maximum.

In order to test this conclusion the amplitude ratios for best beats were observed for electrical stimulation of the finger tip. Referring again to Fig. 13-46, we find that the slope of the curve for electrical stimulation is similar to that obtained for mechanical stimulation. In general, the amplitudes obtained for best beats for the harmonics were larger because the available amplitude range for electrical stimulation was small. The high levels were painful, and subjects sought to avoid the pain threshold.

A further test to show that the amplitude of best beats is to a large degree independent of the physiological condition of the sense organ is to determine the best beats for the second harmonic in different octave bands in which the sensitivity of the sense organ increases, decreases, or remains constant. In Fig. 13-50, the upper curve shows the threshold for sinusoidal vibrations on the finger tip. In the lower drawing the ordinate gives the relative ratios of the amplitude of the second harmonic to the amplitude of the fundamental giving the best beats. The ratios show only small variations. They are larger for the insensitive frequency range because of the smaller available intensity range.

Although the amplitude ratio that produces the best beats seems to be a property of the stimulus, this is not true of the magnitude variations. We may expect that, as the frequency increases, the nerve impulses, because of refractory phase, are no longer able to follow the amplitude during the short time of its peak, and for this reason the increase of magnitude during the peaks is less pronounced. Subjects were asked to compare the magnitude of the beat sensation at low frequencies with the beats at higher frequencies and to estimate the magnitude of the high-frequency beats relative to the low-frequency beats. The results are shown on the left of Fig. 13-51 for the finger tips of two observers.

Above 100 cps there was an appreciable diminution in the size of the beat sensation, and above 1000 cps the beats became so small as to be barely noticeable. The smallness of the beats made it impossible to carry the measurements of Fig. 13-51 above 600 cps. Probably the sudden increase in the threshold in Fig. 13-50 above 500 cps reflects the fact that the nerve impulses were no longer able to follow the rapid variations of amplitude.

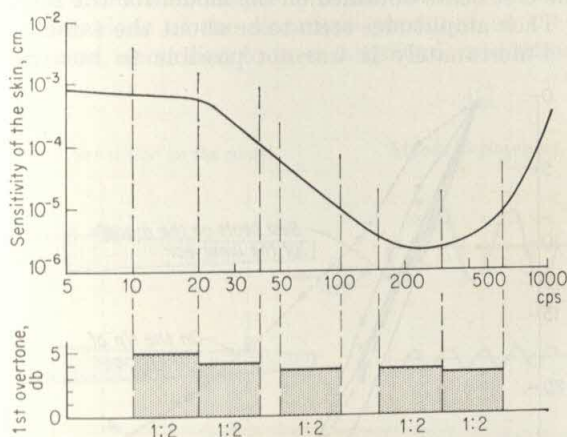


FIG. 13-50. Relation between the threshold sensitivity of the skin (upper graph) and the condition for best beats between a fundamental and its second harmonic (lower graph).

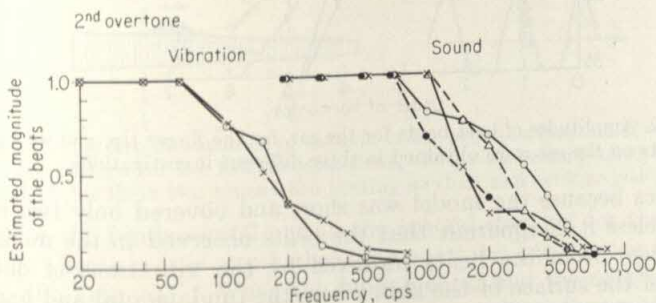


FIG. 13-51. The estimated magnitude of best beats as a function of frequency, for vibration on the finger tip and for sounds.

As the threshold of hearing begins to rise only above 4000 cps, the elements of the auditory nervous system should have a relatively short refractory phase. When this experiment was repeated with pure tones, the curve shown on the right side of Fig. 13-51 was obtained. The magnitude of the sensation of best beats was constant up to about 700 cps, and above 6000 cps beats were again observed with difficulty. The frequency range in the auditory system seems to extend about ten times higher than the vibratory sensation in the finger tip.

Harmonics in the Model and in the Ear. The model of the inner ear, enlarged according to dimensional laws and supplied with the skin of the arm as a sense organ, has proved useful in investigating many details of hearing. Therefore the amplitudes of best beats were determined on the model by exactly the same method used to determine harmonics in hearing. The thin lines in Fig. 13-52 show the amplitudes for best beats in hearing as obtained by three different authors. The heavy line shows the best beats obtained on the model for the second and third harmonics. Their amplitudes seem to be about the same as those found in hearing. Unfortunately it was not possible to measure the higher

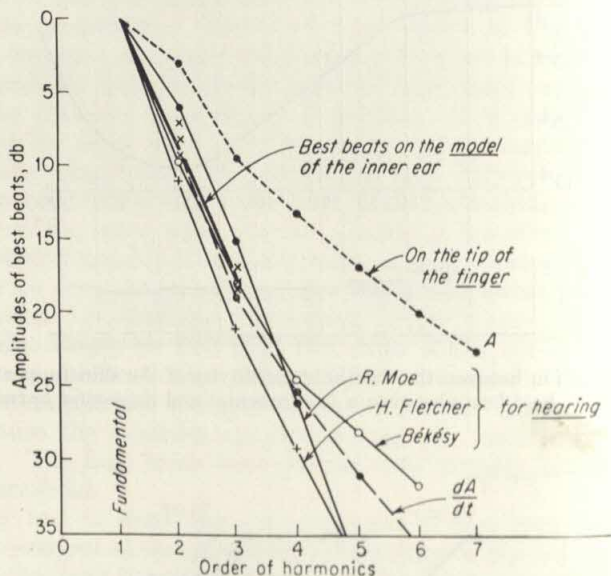


FIG. 13-52. Amplitudes of best beats for the ear, for the finger tip, and for the model. The results on the ear were obtained in three different investigations.

harmonics because the model was short and covered only two octaves. Nevertheless it is apparent that the beats observed in the model must be different from the beats observed by the vibrations of one small section of the surface of the skin where the fundamental and harmonics stimulate the same area.

We know from Fig. 13-48 that the first derivative of the sum of the fundamental and the third harmonic has a maximal value for a certain amplitude ratio. If we compare the amplitudes of the best beats in hearing with the first derivative of the amplitudes of the sum of the fundamental and third harmonic, we see in Fig. 13-52 that the first derivative has almost the same values as the best beats found in hearing. It might seem reasonable, therefore, that in the model and in hearing also the first derivative is the stimulus for the perception of best beats. But closer observations with the model showed that this assumption is not correct.

There is a large difference between the beating sensation on the finger tip and on the surface of the arm resting on the vibrating membrane of the cochlear model. On the finger tip the beats are recognized as amplitude variations, whereas on the arm resting on the model the beats manifest themselves mostly as a change in the place of stimulation along the arm. This difference is illustrated in Fig. 13-53. The shaded areas on the left side of the figure represent the basilar membrane with its width increasing from the "stapes" (in the middle of the drawing) to the left. The locations of the sensations produced on the skin of the arm are represented, according to their magnitude and shape, in the top

1:2

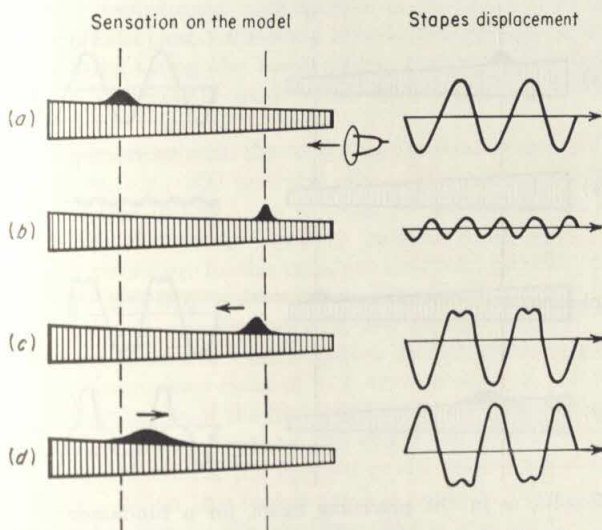


FIG. 13-53. The pattern of sensation of the skin of the arm as a function of waveform: (a) shows the pattern for the fundamental alone, (b) for the second harmonic alone, and (c) and (d) for these two tones when beating at their two extreme positions.

drawing for the fundamental and in the second drawing for the second harmonic. Because it is at a higher frequency the harmonic is localized closer to the "stapes." When the fundamental and the overtone were presented simultaneously, the locus of the sensation during the beats periodically oscillated between the two positions shown in the two lower drawings. The extreme positions both lie between the positions obtained from the single tones, and they are more spread out than the sensations obtained for pure sinusoidal vibrations. From this it seems that when the arm is resting on the membrane, an upward displacement of the membrane produced by a displacement of the "stapes" to the left feels stronger than a downward displacement. When the top of the combined displacement is flat, as in the third drawing down, the two rapid vibrations of the time pattern are felt, and the sensation is localized in the neighborhood of the "stapes." When during the beating the phase of

the harmonic is reversed and the harmonic amplitude is added to the maximum of the fundamental, the upward displacements of the membrane have a low periodicity (as the lowest drawing shows), and the sensation is located to the left side of the membrane.

The same observations were made for a frequency ratio of 1:3, with results given in Fig. 13-54. Because the distance between the frequencies was larger the sensation during the best beats remained closer to the sensations obtained for the sinusoidal vibrations. During the oscillations

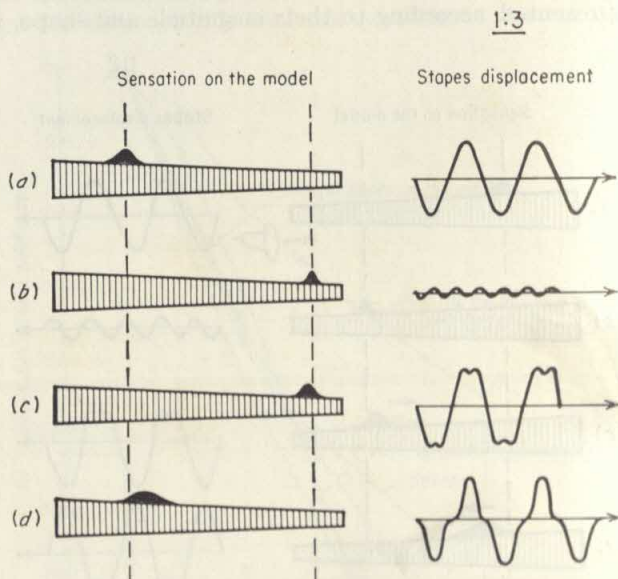


FIG. 13-54. Results, as in the preceding figure, for a fundamental and its third harmonic.

of the locus of the sensation from the extreme position of one side to the other side, the intermediate stages in the frequency ratio 1:3 were more difficult to observe than for the ratio 1:2, and this gave the impression of a jump.

The adjustment of the amplitude of the harmonics for best beats is a delicate one, and 2 or 3 db can make a large difference in the displacement of the locus of stimulation. But with a proper adjustment there was the impression that the amplitude modulation during the beats was almost negligible compared with the sensation of the oscillations of the locus. However, if the attention was directed to the region near the "stapes" or to the region near the "helicotrema" and there were more than three beats per second, there was a tendency to suppress the rapid lateral oscillations along the surface of the arm and to observe an intensity variation at the place where the attention was focused. A disturbing effect during these observations was an adaptation of the skin for vibrations, which was much more pronounced than the adaptations of the ear. It

was frequently necessary to interrupt the observations and rest. In most of the observations the frequency of the fundamental was 50 cps. Control observations were done with 20 and 80 cps.

It should be mentioned that, during all these observations on the model of the ear, the "pitch" of the vibrations as such hardly came to consciousness because the place of the stimulus on the arm was the predominant sensation.

In spite of the fact that the "pitch" of the vibration was not observed directly, all the beating phenomena experienced with the model agreed with those observed in the ear. From this correspondence it seems clear that the periodicity of the nerve impulses does not play an important part in the production of beats, and that the place of maximal sensation along the basilar membrane corresponds to pitch in hearing. At the same time it is certain that volleys are fired in the rhythm of the periodicity of the vibrations along the nerve fibers leading to the higher neural level. Keidel (2,3) recently made some observations of volleys on the skin of the frog.

After these experiences with the model, beats were observed for tones at several frequencies, *e.g.*, 200 and 600 cps. The same phenomena were observed as with the model. As in Figs. 13-53 and 13-54, during the beats the pitch of the tonal complex oscillated between two values. When the sound pressure in the external auditory meatus was given a pattern similar to the upper drawing in Fig. 13-47 for $\phi = 0$ the pitch was high, and when it corresponded to the pattern of $\phi = \pi$ the pitch was low. Because positive and negative sound-pressure patterns are the same for the frequency ratio of 1:3, the polarity of the earphone is unimportant. It is not so if the frequency ratio is even, such as 1:2. As already seen in the observations on the finger tip (Fig. 13-49), a pull or push on the finger may favor the upward or the downward movements of the vibrating rod. With this technique it is possible to discover whether there is a resting tension in the sensitive cells of the ear which is always superimposed on the vibrations and favors a displacement in one direction.

For this purpose five subjects were asked to indicate whether the loudness of beats between 200 and 401 cps was maximal when the sound pattern in the meatus was like the pattern for $\phi = \pi/2$ or $\phi = 3\pi/2$ in Fig. 13-49. The subject could observe the sound pressure in his meatus on the oscilloscope. Most of the subjects made a definitive statement one way or the other, but sometimes after a few hours they reversed their statement or were no longer sure about it. From this it seems that in the normal ear there is no mechanical resting tension in the sensitive cells, or at most there are only small fluctuations about a zero value. It would be interesting to repeat these experiments on patients diagnosed as having a "hypertension in the cochlea." Perhaps by this means it might be discovered whether the blown-up Reissner's membrane often seen in histological sections of the organ of Corti is an artifact or whether it is a consequence of tensions in the inner ear.

In conclusion it may be pointed out that in electronics the search tone has provided a highly successful method for performing harmonic analyses

of complex sounds. The adjustment to best beats makes it possible to estimate the relative amplitudes of the different components. From the point of view of measurements it seemed reasonable to apply this technique to the determination of the nonlinear distortions of the ear, provided that the ear was capable of isolating the observed harmonic from the complex sound with such accuracy that the amplitude variations of the harmonic would be recognized, undisturbed by the other sounds. In technical equipment this isolation is achieved by the use of a filter. It turns out, however, that neither the skin nor the ear has such an ability of frequency discrimination, and therefore some other factor produces beats larger than the beats produced by the harmonics. Consequently it must be concluded that the method of best beats does not give a measure of the overload of the organ of Corti. An earlier paper has to be corrected in this respect.* In the ear the best beats are determined largely by the difference limen for loudness and pitch, and this is probably the reason why in pathological cases these beats are related to recruitment, as mentioned by Ophelm and Flottorp.

The situation does not alter measurements made with beats or their usefulness for diagnostic purposes. But it means that the definition of nonlinearity, as used in electronics, cannot be applied to the ear by using loudness as an indicator. To what degree conclusions drawn in the study of harmonics apply to difference tones will have to be investigated separately. The same holds for the clinical diagnosis of nerve deafness. The combined frequency and amplitude modulation obtained by the method of best beats, as investigated by Lawrence and Yantis, may have some technical or clinical advantages over the simple amplitude or frequency modulation.

The complicated nature of beat phenomena in a complex wave can be seen if we observe the beats of different waves. Figure 13-55 shows the harmonics calculated for three different wave patterns. The square wave has no second or fourth harmonic and represents the maximal overload of a sinusoidal wave. Yet if we listen to it, the square wave beats with the fourth harmonic. In the ear this may be a consequence of phase distortion. To avoid any type of distortion an electric square wave with precise corners was used as a stimulus. When the fourth harmonic was superimposed upon this square wave the maximum of the amplitude remained constant. The experiences with sinusoidal variations therefore suggested that no beats would be observed during electrical stimulation

* See p. 332. There seem to be three ways in which best beats can arise between a fundamental and a harmonic: (1) mechanically in the ear, (2) by a pure tone in the auditory nervous system, and (3) as an amplitude ratio between the harmonic and the fundamental representing the pattern of vibration of the sum of the fundamental and the beating search tone. Twenty years ago the author assumed that only the first two possibilities had to be considered. As it is possible to decrease the loudness of the fundamental considerably by fatigue without at all affecting the amplitude ratio producing best beats, it now appears that these beats arise in the ear through mechanical processes and are independent of the state of the nervous system. The author now believes that the third possibility predominates, and the method of best beats does not give any information regarding nonlinearity in the ear.

of the finger tip. Experiments showed, however, that beats were observed, and their sensory magnitude increased continuously as the amplitude of the harmonic was increased, without exhibiting an optimum. If the oscilloscope was observed as the current was passed through the skin, it was found that the sensation of maximal stimulation was obtained just at the moment when the maximal steepness of the harmonic was added to the steepness of the square wave (see Fig. 13-56).

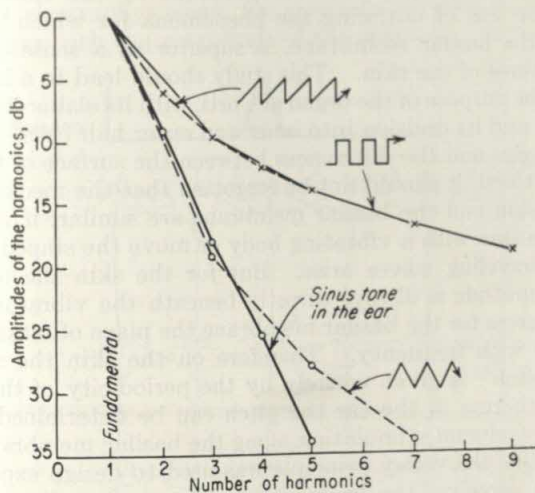


FIG. 13-55. Measurements of harmonic amplitude by the best-beat method, for different waveforms as indicated.

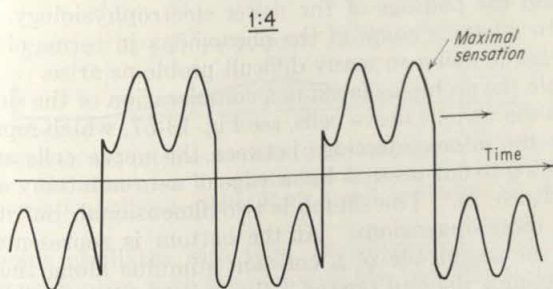


FIG. 13-56. Effects of superimposing a fourth harmonic on a square wave.

The simple rule found for the harmonics of a sinusoidal vibration, namely, that the magnitude is determined during the beats by the peak of the amplitude, is not correct for vibratory patterns with a steep front, as in a square wave. Here the steepness produces the maximal nerve excitation. Unfortunately we know very little about the way in which a steep wavefront, as in a square wave, is transmitted to the inner ear or how it travels along the basilar membrane. Consequently we do not

have the fundamental facts that would permit an analysis of the beats of complex patterns.

NEURAL VOLLEYS AND SIMILARITIES BETWEEN TONAL AND CUTANEOUS SENSATIONS*

The following section continues the investigations of similarities between hearing and the sensations produced by the vibrations of the skin, with the aim of outlining the phenomena for which the organ of Corti, with the basilar membrane, is superior as a sense organ to the simple structures of the skin. This study should lead to a better understanding of the purpose of the organ of Corti, with its elaborate anatomical arrangement and its division into inner and outer hair cells. In evaluating the analogies and the differences between the surface of the skin and the organ of Corti, it should not be forgotten that the mechanical vibrations of the skin and the basilar membrane are similar: if we touch the surface of the skin with a vibrating body or move the stapedial footplate of the ear, traveling waves arise. But for the skin the maximum of vibratory amplitude is always directly beneath the vibrator for all frequencies, whereas for the basilar membrane the place of maximum vibration changes with frequency. Therefore on the skin the sensation of vibratory "pitch" is given entirely by the periodicity of the volleys in the nerves, whereas in the ear the pitch can be determined further by the place of maximum stimulation along the basilar membrane.

On the whole, the volley principle was used to design experiments on how the skin perceives the frequency and locus of a vibrator. In this approach an attempt was made to find a connection between a purely phenomenological description of the experiences of hearing and skin perception and the findings of the newer electrophysiology. It should be possible to interpret some of the phenomena in terms of neural discharges, though in doing so many difficult problems arise.

To illustrate the problems faced in a consideration of the simple neural discharges in the various nerve cells, see Fig. 13-57, which represents in a sketchy way the interconnections between the nerve cells and the end organs according to our present knowledge of neuroanatomy and electrophysiology (Ruch, 2). The sketch is two-dimensional, but it should be extended to three dimensions. At the bottom is represented the distribution of the magnitude of a constant stimulus along the surface of the skin containing the end organs. Groups of end organs are interconnected by nerve fibers. The end organs are interconnected with one another, and it may happen that one end organ is connected to two or more different nerve fibers. Interconnections running parallel to the surface of the sense organ are found not only in the skin but also in the ear and eye to a more or less developed degree. As a whole they constitute a plexus. The ascending nerve fibers lead to a layer of ganglion cells, and the cells are laterally interconnected. The same situation is

* Article 81 as listed in the Author's Bibliography. Published in 1957.

repeated several times. The top of the figure indicates that the lateral spread of the sensation seems to be smaller than the spread of the stimulus. This is certainly true for skin sensations, for a vibrator may produce traveling waves that extend for great distances along the surface of the skin, as may be seen by stroboscopic illumination. Nevertheless, only the skin below the vibrator is felt as vibrating (Keidel, 3).

In the lower part of the figure the neural discharges are shown in the nerve fibers coming from the end organs. According to our present knowledge of electrophysiology, for a steady stimulus the rate of discharge increases with the magnitude of the stimulus. If the magnitude

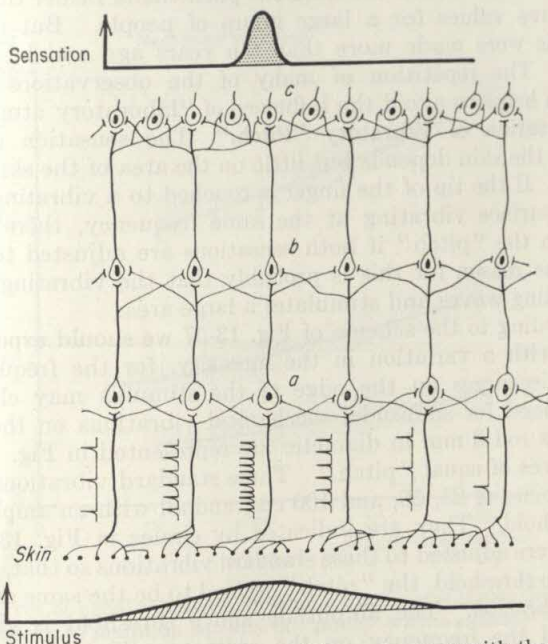


FIG. 13-57. Sketch of the interconnections of the end organs with the nerve cells at various levels. Also shown are the spatial distributions of the stimulus (below) and the resulting sensation (above). After Ruch, based on numerous studies.

of the stimulus oscillates with time, the discharges come in bursts or volleys in synchronism with the period of the oscillations, provided that the stimulus is sufficiently strong. On the edges of the stimulus, however, it may happen that the frequency of the stimulus is higher than the frequency of the discharges. Then only every second or third cycle of the stimulus is able to produce a discharge, and the periodicity of the discharges is smaller on the edges of the stimulus than in the middle. Under these conditions we may expect the sensation of vibratory "pitch" on the skin to be determined not only by the frequency but also by the intensity and local distribution of the stimulus along the skin surface. The experiments showed this conclusion to be correct.

The electroanatomical scheme of Fig. 13-57 suggests many experiments along the lines of three main problems: (1) How is the sensation of vibratory "pitch" correlated with the frequency of the stimulus? (2) How is the location and lateral spread of the sensation determined by the stimulus? (3) How is the magnitude of the sensation influenced by the stimulus? Only experiments related to questions (1) and (2) will be considered here, because magnitude is a most difficult question in relation to our present knowledge of electrophysiology.

It should be mentioned that some of the experiments were made on only three or four subjects, because the chief interest was in working out the relations between the different phenomena rather than obtaining representative values for a large group of people. But many of the observations were made more than ten years ago and have now been rechecked. The repetition of many of the observations in different laboratories helps to avoid the influence of "laboratory atmosphere."

The Sensation of Vibratory "Pitch." The sensation of vibratory "pitch" on the skin depends but little on the area of the skin exposed to vibrations. If the tip of the finger is touched to a vibrating needle and then to a surface vibrating at the same frequency, there is hardly a difference in the "pitch" if both sensations are adjusted to be equally strong. The reason for this is probably that the vibrating needle produces traveling waves and stimulates a large area.

But according to the scheme of Fig. 13-57 we should expect the pitch to change with a variation in the intensity, for the frequency of the bursts of discharges on the edge of the stimulus may change. The values obtained for sinusoidal mechanical vibrations on the tip of the finger with a rod 3 mm in diameter are represented in Fig. 13-58 in the form of curves of equal "pitch." Three standard vibrations were used, with frequencies of 25, 50, and 100 cps, and all with an amplitude 20 db above threshold. They are indicated by circles in Fig. 13-58. Other vibrations were adjusted to these standard vibrations so that, for different values above threshold, the "pitch" seemed to be the same as that of the standard vibration. The amplitude above threshold is given on the abscissa and the frequency on the ordinate. The crosshatched area along the curves of equal "pitch" represents the spread of the observations for different subjects. As there is always a chance that the sensations on the tip of the finger are modified by the tendons and muscles below the skin, the measurements were repeated on parts of the body with no underlying tendons or muscles. The general slope of the curves of equal "pitch" remained the same.

Figure 13-58 shows that, when the frequency of vibration was kept constant, an increase in the vibratory amplitude produced an apparent drop in the "pitch." In order to keep the "pitch" equal to that of the standard, the frequency of the vibrations had to be increased. This drop in "pitch" as the amplitude increased is not inconsistent with the scheme represented in Fig. 13-57. Surely for continuous stimulation with increasing amplitude, the rate of the neural discharges increases, as has been found over and over again. But when the vibrations are

alternating, the main phenomena are different. When the alternating vibrations are small, the neural discharges may have a smaller frequency than the stimulus itself. Owing to the refractory periods, the discharges are out of synchrony with the stimulus and are irregular. Since there are several nerve tracts, the asynchronous discharges produce a sort of white noise, and the "pitch" of this white noise is higher than the "pitch" of the sinusoidal stimulus. With increasing amplitude of the vibrations, the discharges become more and more synchronous with the vibrations, and the somewhat smoother sensation produced by the white noise becomes increasingly rough, with a time pattern that produces a

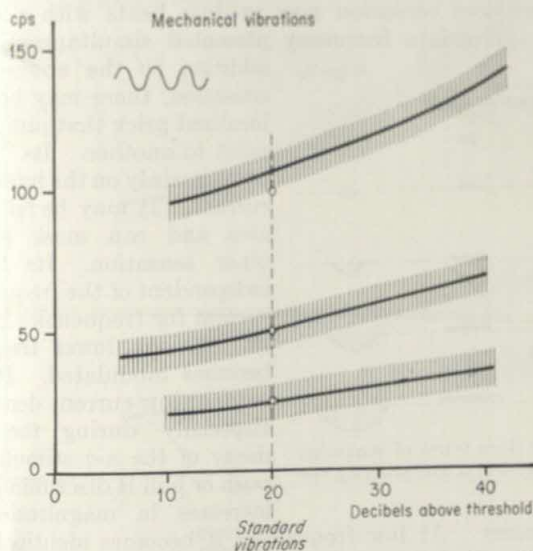


FIG. 13-58. Curves of equal vibratory "pitch." Each curve shows the variations in frequency necessary to maintain equality of "pitch" with a standard of 25, 50, and 100 cps at 20 db above threshold.

sensation of lower "pitch." This gradual change from smoothness to roughness with increasing loudness can be observed in many situations.

If the change in the type of neural discharge is responsible for the change in "pitch" with increasing intensity, then it should be irrelevant whether the stimulus is produced by mechanical vibrations or by stimulation with alternating current. The difficulty with stimuli produced electrically is that they are more diffuse than those produced mechanically, and electrical stimulation therefore produces not one but several different simultaneous sensations that are sometimes difficult to separate.

First of all, with electrical stimulation we have to consider that both electrodes may produce a stimulus, and we must first make sure that the resulting stimulus on the skin occurs at the place to which we are referring and is not masked by a stimulus produced by the second electrode at a

different place. In a larger frequency and amplitude range, it is sometimes difficult to avoid the masking effect of the second electrode. The use of a large contact surface, or even the splitting of the electrode into two or more electrodes placed at different points, may help to satisfy the requirement of an indifferent electrode.

In addition, the current may produce several sensations with different magnitude relations, especially when the frequency and amplitude ranges are large. (1) There is a sensation directly beneath the electrode that is identical with the sensation produced mechanically. It changes its "pitch" with frequency and intensity, and it is sometimes impossible to tell whether it has been produced mechanically or electrically. This electrically produced sensation may produce beats with a mechanical vibration of appropriate frequency presented simultaneously. (2) In addition to the above-mentioned sensation, there may be a sharply localized prick that jumps from one point to another. Its "pitch" depends mainly on the intensity of the current. It may be felt on a large area and can mask almost any other sensation. Its "pitch" is independent of the frequency of the current for frequencies higher than 20 cps. At lower frequencies it becomes modulated. It does not occur at low current densities. (3) Especially during the onset or decay of the a-c stimulus, a small push or pull is discriminated, which increases in magnitude with in-

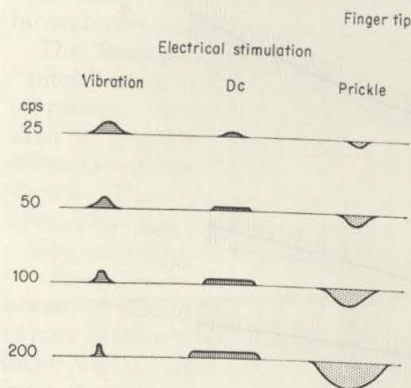


FIG. 13-59. The three types of sensation produced by electrical stimulation on the finger tip.

creasing frequency. At low frequencies it becomes identical with (1). (4) It should be further mentioned that the pulls may be disturbing during observations at lower frequencies.

It is fortunate that the relative intensity of these different sensations is sometimes different on different sections of the skin, and therefore it is possible to make clear observations in spite of them. Figure 13-59 shows how one subject found the different sensations produced by an electrical current applied to the tip of the finger to vary in extent as the frequency varied.

After the subjects learned to discriminate the different sensations, the curves of equal "pitch" for sensation (1) were determined, using for comparison the mechanical standard vibration represented in Fig. 13-58. The results for electrical stimulation as shown in Fig. 13-60 gave a slope closely similar to that found for mechanical stimulation as shown in Fig. 13-58. Both series of observations were made on the tip of the finger. This similarity leads to the conclusion that the neural discharges for mechanical and electrical stimulation are about the same, for it holds for other sections of the skin also.

The interesting thing noted in these observations is that the change in "pitch" with intensity seems to be completely continuous. If a larger number of neural groups were in phase with the stimulus, we should expect that, in accordance with the role of the refractory phase of the nerves, there would be some jumps in "pitch" during the intensity increase. Since this seems not to be so, the question arises whether there are still other nerve groups that could be synchronized. This possibility was tested by using square vibrations, either mechanical or electrical ones. Because of the sharp onset, the synchronization of the discharges for these stimuli should improve. As Fig. 13-61 shows, this is

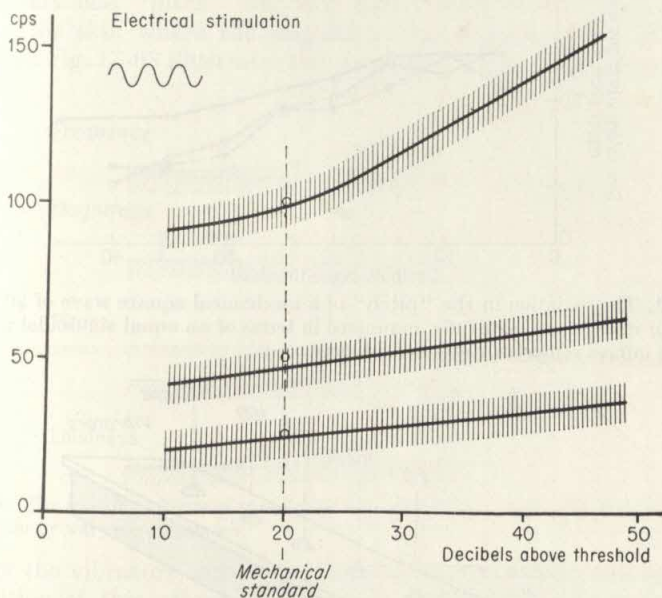


FIG. 13-60. Curves of equal vibratory "pitch" for electrical stimulation. Compare with Fig. 13-58.

indeed the case. A square vibration with a constant frequency of 20 cps was matched with a sinusoidal vibration so that the sensory magnitude and the "pitch" seemed to be equal. When this was done at different levels of intensity, two relations emerged. (1) The "pitch" of the square vibration decreased with increasing intensity, relative to the sinusoidal vibrations. Hence for sinusoidal vibrations 40 to 50 db above threshold the synchronization is still not complete. (2) When the square and sinusoidal vibrations were matched for "pitch," the periodicity of the sinusoidal vibrations was about twice the frequency of the square vibrations. In terms of neural discharges, this means that in a sinusoidal vibration during one full period only one volley of discharges is produced. In the square vibration, on the other hand, two volleys are produced during a full period, one during the upward movement of the vibrator. This is in agreement with electrophysiological experience, which shows

that rapid changes in the stimulus are more likely to produce a volley than slow ones. Thus on the finger tip square vibrations at the given frequencies may produce a volley during the movement in each direction, in contrast to the sinusoidal vibration, which acts only in one direction.

In hearing there are pitch changes of pure tones with increasing intensity, but they are of much smaller magnitude. This difference indicates that the pitch sensation in hearing is not produced by the volleys in the same way as the pitch sensation on the skin.

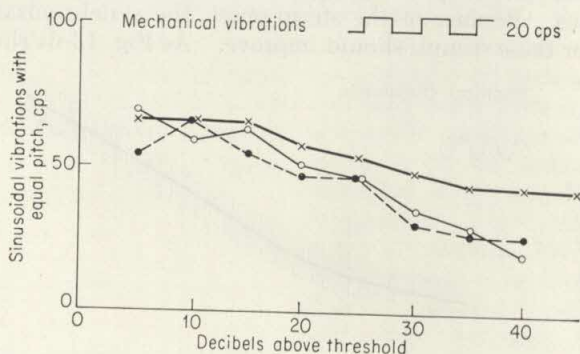


FIG. 13-61. The variation in the "pitch" of a mechanical square wave of 20 cps as a function of its level of magnitude, expressed in terms of an equal sinusoidal vibration. The three curves represent different subjects.

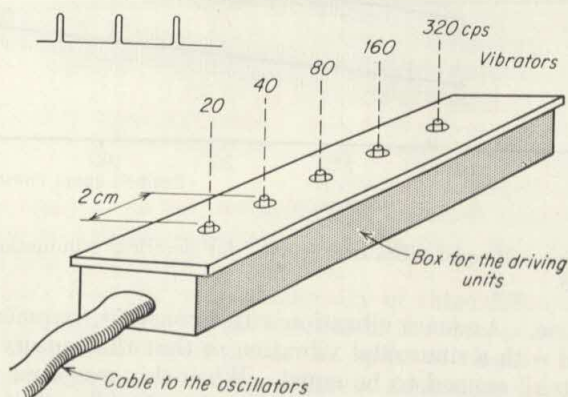


FIG. 13-62. Arrangement of a series of vibrators to show inhibition.

Summation of Vibratory Stimuli with Different Frequencies. From the scheme of Fig. 13-57, it can be seen that for sinusoidal vibrations the frequency of the volleys is smaller on the edge of the stimulus than in the middle. Thus along the surface of the skin there are simultaneous volleys of different frequency. This raises the question as to what happens to the volleys whose frequencies differ from those along the majority of the neural pathways. In a preliminary experiment on this question, a set of vibrators was placed 2 cm apart along a line, as shown in Fig. 13-62. The vibrators were driven by short clicks that increased

in frequency from left to right, each vibrator one octave higher than its left-hand neighbor. The lowest frequency was 20 cps and the highest 300 cps. The tips of the vibrators touched the surface of the skin. The intention was to stimulate only sharply defined areas on the surface of the skin and to avoid traveling waves along the skin by pressing the solid plate against the skin's surface. The amplitudes of the vibrators were adjusted so that when they were presented separately each produced a sensation of the same sensory magnitude. The stimulus along the skin may be represented by the upper drawing of Fig. 13-63.

The sensation produced by such a stimulus pattern was extraordinary in that only one "pitch" was felt; this "pitch" corresponded to the place on the skin where the magnitude was concentrated. The lower drawing in Fig. 13-63 illustrates this situation. Increasing the amplitude

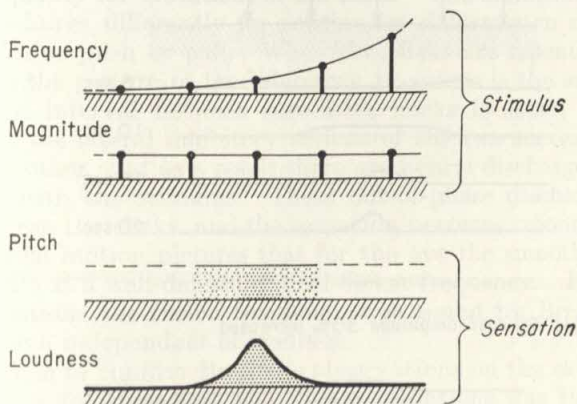


FIG. 13-63. The sensory effects of presenting five vibrations to the skin simultaneously, with frequency varying as shown.

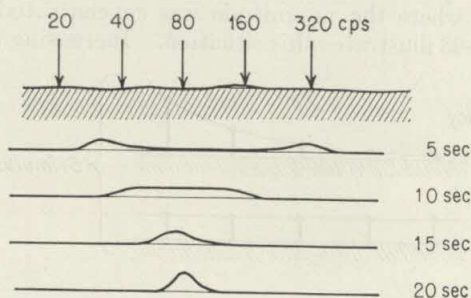
of one of the vibrators caused the location of the sensation to approach the position of this vibrator. However, not only the location of the sensation moved toward that vibrator, but also the "pitch" came closer to the "pitch" that would be produced if that vibrator were presented alone.

From this we conclude (1) that, as a consequence of the interaction between the volleys of different frequencies, the "pitch" is determined to a large degree by the "pitch" of the volley with the maximal magnitude. The frequency patterns of all the other volleys are inhibited and disappear from the picture. (2) We have to conclude further that, in spite of the fact that the frequency pattern of the volley disappears, this is not true of the magnitude contribution of that volley, because the switching on and off of the vibrator at either extreme end changed the magnitude of the sensation without affecting the "pitch." Thus up to a certain distance from the locus of the sensation we have "pitch" inhibition with a simultaneous summation of magnitude.

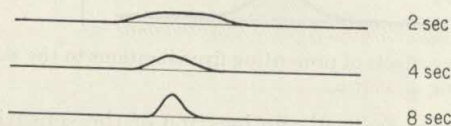
When the skin of the lower arm was stimulated by vibrators 2 cm apart, it was possible to determine how the inhibitory interactions

developed after the onset of the stimulus. This situation is shown in the upper drawing of Fig. 13-64 for five equally "loud" vibrators at frequencies ranging from 20 to 320 cps. For a few seconds after the onset of the stimulus, the vibrators at 20 and 320 cps were felt separately, each at its own "pitch" and each in its own place. But after only 10 sec the whole stimulus flowed together toward the center, and a sharply defined maximum appeared whose "pitch" corresponded to the vibrator in the center. However, a long build-up of the sensation was difficult to achieve. As little as a 30 per cent increase in the vibratory amplitude

(a) All frequencies equally loud



(b) 80 cps: amplitude 30% increased



After the oscillators
were turned on

FIG. 13-64. The form of distribution of sensation produced by the situation shown in the preceding figure, (a) as a function of time and (b) as a result of emphasizing the middle vibrator.

of the center vibrator at 80 cps made it impossible to feel the two end vibrators separately, and the central maximum became apparent almost immediately (Fig. 13-64b). The build-up time could be made still smaller by moving the vibrators from the lower arm to more sensitive areas near the finger. Even after all the vibrators were carefully adjusted to equal magnitude when presented separately, the build-up time was often four to five times smaller on the finger than on the lower arm.

All the experiments described above were repeated with electrical stimuli. The solid plate in Fig. 13-62 was grounded and attached to the indifferent electrode on the body. The vibrators were isolated and the tips served as stimulating electrodes. The electric field was sharply localized because the current flowed from the vibrator tip to the

edge of the opening, a distance of less than 1 mm. The inhibitory effects obtained for "pitch" and the summation for magnitude were the same as for mechanical stimulation.

It is obvious that the experiment described above is important for an understanding of the neural functioning of the inner ear. This too shows that even a flat maximum is enough to set in action inhibitory effects that determine the pitch and lateral spread of a sensation. Neurologically there seems to be no need to sharpen the amplitude distribution of the vibrations along the basilar membrane by a better mechanical filter action of the membrane. The present flat maximum of the traveling waves seems to be enough to set the inhibitory effects in action and to produce the final sharp localization of the distribution of sensation along the organ of Corti.

Fusion Frequency for Vibrations of the Skin. The inhibition along the nerve tract behaves differently for continuous deformation of the skin than for a sudden push or pull. When the clicks are repeated at long time intervals the picture of the inhibitory processes is the same. But when the time interval between successive clicks is short, there is a moment when the lateral inhibitory actions of the two successive clicks influence each other, and as a result there are neural discharges that are out of phase with the stimulus. These out-of-phase discharges fill in the gaps between the clicks, and the sensation becomes smoother. It is well known from motion pictures that for the eye the smoothing of the sensation occurs at a well-defined critical flicker frequency. For hearing and skin sensations the fusion frequency was found by Brecher to be about 18 cps and independent of loudness.

It was possible to confirm Brecher's observations on the skin, and the fusion frequency for sinusoidal and square vibrations was the same as for a series of spikes. It did not matter whether they were presented mechanically or electrically. A change in amplitude of 20 db produced a maximal increase in fusion frequency of about 5 per cent. Also the fusion frequency was independent of the size of the stimulated area. However, the fusion did not occur in one single step, and the fusion frequency was different for different sections of the skin.

Measurements of fusion frequencies for a sensitive and an insensitive spot on the chest are shown in Fig. 13-65*a* and *b*. In these measurements the smoothness of the sensation produced by the vibration was observed for square vibrations and recorded as the ordinate on an arbitrary scale. For frequencies below 5 cps, each movement of the vibrator was felt separately, and there was almost no feeling of continuity of stimulus. As the frequency was increased the sensation of smoothness increased in several discrete steps until a maximum was reached, and then there was a continuous increase in smoothness with increasing frequency. The figure represents as nearly as possible the relative magnitude of the sudden changes in smoothness. In general, there was a large step, and above and below it a smaller one. The frequencies at which these steps occurred were well defined: the lower fusion frequency was about two-thirds the fusion frequency of the maximal step, and the higher one about

four-thirds. The fusion frequencies were lower for skin areas with high sensitivity and increased continuously as the point of measurement was moved into skin areas with lower sensitivity, but the ratio between the different fusion frequencies remained the same. A similar shift in the fusion frequencies occurred when the sensitivity of the skin was changed artificially either by fatigue and adaptation or by anesthesia. Rapid fatigue and adaptation is the reason some observers find a shift in the fusion frequencies during observation.

To study the effect of anesthesia on the fusion frequency, the finger tip was cooled for about 3 sec by an ethyl chloride spray. The finger tip was then brought into contact with a vibrator set at a given frequency.

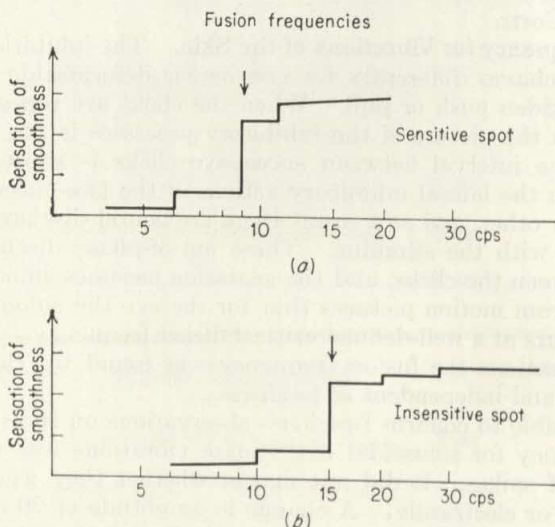


FIG. 13-65. Critical flicker frequency for two regions of the skin. The steps indicate that fusion occurs in several stages.

Immediately after the freezing, the sensation on the finger tip was rough, indicating that the frequency was below the fusion frequency. But after a few seconds of recovery the sensation suddenly became smooth, which means that at that moment the fusion frequency was lower than the set frequency. In this way it was possible to determine how the fusion frequency decreased with the increase in recovery time. Measurements made on three observers are shown in Fig. 13-66. For complete recovery, many minutes were usually necessary, and sometimes even as much as a half hour if there had been repeated freezing. For most observations, square vibrations or series of pulses were used, because the fusion frequency is much more sharply observable for them than for sinusoidal vibrations.

Rotating Skin Sensations Analogous to the Rotating Tone in Hearing. As the frequency was increased far beyond the fusion frequency, the smoothness of the sensation still increased continuously until it reached

the point at which the sensitivity of the skin dropped and further stimulation was impossible. This indicates that, even far beyond the fusion frequency, there are still volleys present that are in phase with the stimulus, just as has been found in electrophysiology (Keidel, 2). But it

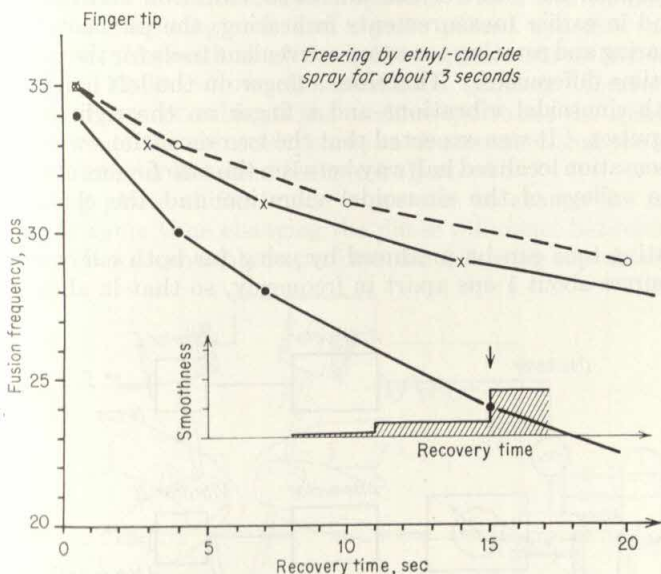


FIG. 13-66. Effects of freezing on the critical frequency of fusion for the finger tip.

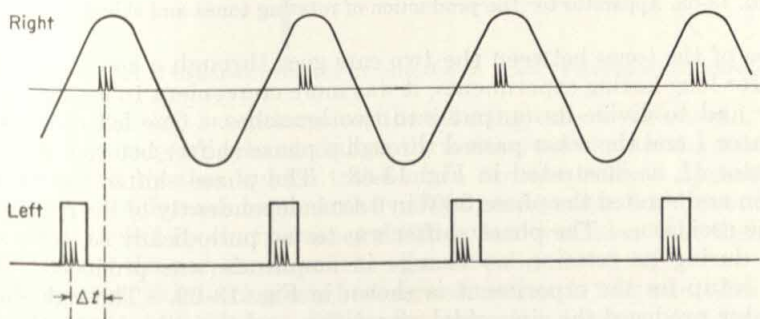


FIG. 13-67. The stimulating situation for producing a rotating skin sensation with a sinusoidal vibration on one finger and a series of mechanical clicks on the other. The small spikes represent neural volleys, and Δt is the interval between them.

should be recalled that the "pitch" sensation is not determined completely by the frequency of the stimulus, because the same vibration can produce a different "pitch" on different places on the skin, and the "diplacuis" between two finger tips that sometimes occurs is much larger than the diplacuis found in normal ears.

If synchronous volleys are produced during the sinusoidal vibrations, for example, in the form shown in the upper drawing of Fig. 13-67, then

the question arises, at what phase of the vibration are the volleys fired? When a series of clicks is presented, as illustrated in the lower drawing of Fig. 13-67, we can assume that the volleys are started during the sharp rise of the click, and the question is, how big is the time delay (Δt in the figure) between the onset of the sinusoidal vibration and the click? As was found in earlier measurements in hearing, the phenomena of directional hearing and rotating tones are convenient tools for the measurement of small time differences. Therefore a finger on the left hand was stimulated with sinusoidal vibrations and a finger on the right hand with a series of pulses. It was expected that the two sensations would fuse into a single sensation localized halfway between the two fingers at the moment when the volleys of the sinusoidal vibration and the clicks coincided in time.

A rotating tone can be produced by using for both ears two different sound sources about 1 cps apart in frequency, so that in about 1 sec the

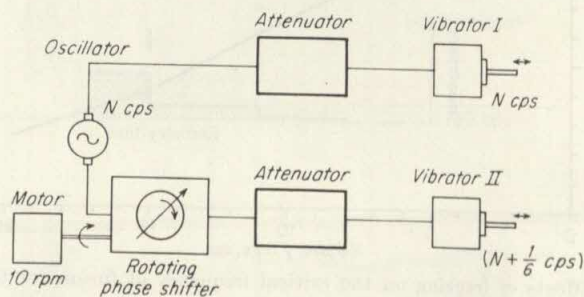


FIG. 13-68. Apparatus for the production of rotating tones and skin sensations.

phase of the tones between the two ears goes through a complete cycle. But for long-lasting experiments, it was more convenient to use one oscillator and to divide its output into two branches. One led directly to vibrator I and the other passed through a phase shifter before it reached vibrator II, as illustrated in Fig. 13-68. The phase shifter was motor-driven and rotated the phase 360° in 6 sec independently of the frequency of the oscillator. The phase shifter was tested periodically to make sure that during its rotation no change in amplitude was produced. The final setup for the experiment is shown in Fig. 13-69. The right-hand vibrator produced the sinusoidal vibrations, and the vibrator on the left side produced the series of sharp clicks, obtained by using the a-c voltage from the phase shifter in Fig. 13-68 to trigger some condenser discharges. After the magnitudes on the two sides were made equal, a well-defined rotating skin sensation was produced at a frequency of 80 cps. This indicates that the volleys produced in both types of stimuli must have many features in common. With a rotating time of 6 sec it was easy to observe the moment at which the sensation was localized exactly halfway between the two fingers. It was found that, for the finger tips, the volleys in the sinusoidal vibration were produced at the maximum of the excursion of the vibrator for a stimulus of 80 cps and an amplitude of

40 db above threshold. This relation did not hold for greater loudnesses or for different frequencies.

In an effort to avoid any phase distortion in the electromechanical driving units, the mechanical vibrations of the vibrating rods were measured directly with a condenser microphone, which was formed by the two tips of the vibrating rods and a plate placed opposite the tips in accordance with the method of the half-resonance curve (Backhaus, 1) shown in Fig. 13-69. Now the excursions of both vibrators added together, and it was possible on the oscilloscope to see the spike exactly at the maximum of the sinusoidal curve at the moment that the sensation was localized halfway between the two fingers.

The rotating phase shifter made it possible to change the frequency without at the same time changing the phase difference between the two sides. Hence it was possible to perform the following experiment. The

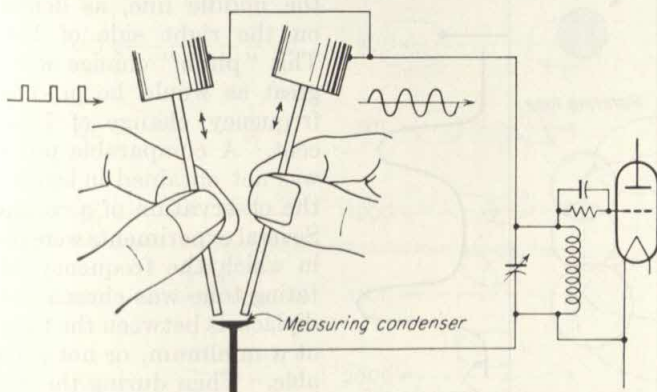


FIG. 13-69. Method of measuring the amplitudes of both vibrators simultaneously.

rotation of the skin sensation or of the rotating tone was observed, and then the frequency was changed abruptly to discover whether the rotation was disturbed by this sudden transient in the frequency. Apparently only the time difference between the volleys is important, for the rotation was not disturbed by the frequency shifts. Care was taken that the relative values of the amplitudes of the vibrators did not change.

The rotating skin sensations had several points in common with the rotating tones, but distinct differences were also present. Let us first consider the rotating skin sensations. If one of the vibrators of Fig. 13-68 was brought into contact with a sensitive area like the tip of the finger, and the other vibrator made contact with a less sensitive area like the ball of the thumb, it was found for discrete presentations that the extent of the vibrations was small on the finger tip and much larger when almost the same frequency was presented to the ball of the thumb. This effect is illustrated in the upper part of the drawing of Fig. 13-70. At the same time, the stimulus on the ball of the thumb seemed to have a higher "pitch." If both stimuli were presented simultaneously and had been made equally strong, the sensation moved periodically from one side to

the other. On the finger tip the spread of the sensation was only a little greater when the stimuli were in the extreme lateral position than when they were presented separately. The same held for the other side. During the transition from one side to the other, the size of the sensation area increased greatly, as indicated by the dotted area in the figure. One of the two transitions through the middle position had a smaller area than the other. This was the transition in which the vibrations on both sides were in phase.

During the rotation, there was a change in magnitude as well as a change in the apparent size of the stimulus. But it is more interesting

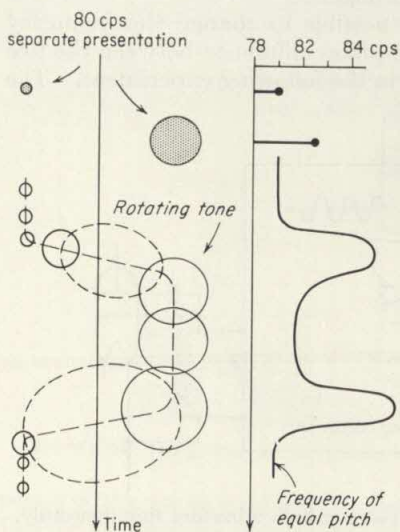


FIG. 13-70. The study of rotating skin sensations. On the left, the passage of the sensation from the finger tip on the left side of the body to an insensitive area on the right side in the course of time, with the size of the sensation indicated by the varying areas; on the right, the changes in vibratory "pitch" during the transit from one side to another.

that in addition the "pitch" of the sensation was changed and it reached a maximum every time the area of the sensation went through the middle line, as demonstrated on the right side of Fig. 13-70. This "pitch" change was often as great as would be produced by a frequency change of 7 to 10 per cent. A comparable pitch change was not obtained in hearing during the observation of a rotating tone. Several experiments were performed in which the frequency of the rotating tone was chosen so that the diplacusis between the two ears was at a minimum, or not even noticeable. Then during the shift of the sound image from one side to the other no pitch change was observed at all. Also with a rotating tone there is no increase in the magnitude of the sound image when the image goes through the middle line. There seems to be a sort of rule, namely, that when the apparent size of the stimulated area increases, the apparent pitch goes up

for stimulation at a constant frequency. If there is no change in the apparent size, then there is no change in pitch.

If we do not take into account the transient through the middle position during the movements from one side to the other, and consider only the extreme lateral position, then there is little difference between the rotating skin sensation and the rotating tone. This becomes evident when we observe the changes in the sensory pattern obtained on the tips of the fingers and for hearing, when the frequency of the rotating stimuli is increased. The results for hearing are shown on the right-hand side of Fig. 13-71, and those for skin sensations on the left-hand side. For the

rotating sound it is well known that the sound image in the extreme positions becomes smaller when the frequency of the tones is increased, up to about 1500 cps. Also, as the frequency is increased, the sound image stays more and more in the medial plane of the head, until for frequencies above 2000 cps it moves only in a small circle around the axis of the head. For low frequencies the sound image moves in the axis of the ears, but as the frequency is increased the sound image is pushed higher and higher, and at 3000 cps it is above the head, as illustrated in the figure.

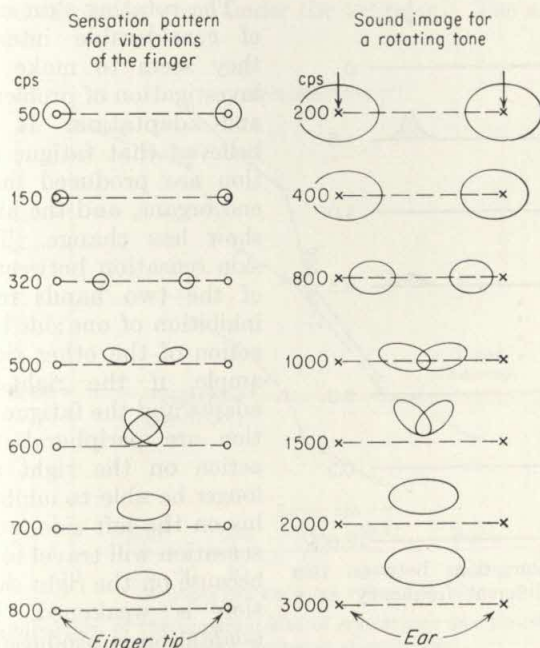


FIG. 13-71. Comparison of rotating vibrations and rotating tones, as a function of frequency.

It was not surprising that, for the skin sensations between the two fingers, the situation is exactly the same. With increasing frequencies the lateral displacements of the apparent sensation became smaller, and at the same time the locus of the sensation moved away from the finger tip toward the body. Corresponding sensory patterns were obtained when the frequencies on the finger were about three times smaller than the sound frequencies.

When investigating the rotating skin sensations it was found possible to produce one if the frequency on one side was two, three, four, or even five times the frequency on the other side ($\frac{1}{6}$ cps was added to produce a periodic phase change) when the magnitudes of both sides were equal. The movements from one finger to the other were distinct. This phenomenon has no analog in hearing. When a tone of 300 cps was presented

to one ear and an equally loud tone of $900 + \frac{1}{6}$ cps to the other ear, no rotating sound image was observed. The two tones appeared completely separated; consequently there was no interaction between the two sides when both tones were equally loud. This seems to prove that in the cochlea there is a frequency analysis that separates these two frequencies from the common neural pathway sufficiently to avoid interaction. This fact holds even if the frequencies on both sides are only one octave apart.

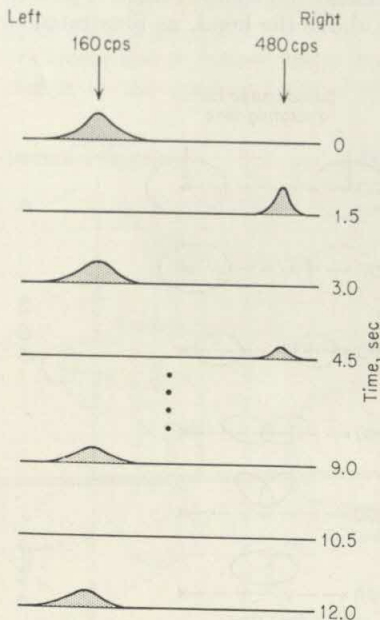


FIG. 13-72. Interactions between two vibrations of different frequency as a function of time.

higher level, above the interconnection of the two sides, then the sensation of the right side will disappear without changing the inhibitory phenomena occurring on the left side.

When the left-hand finger was stimulated by a vibration whose frequency was 160 cps, and the right-hand finger by a frequency of $480 + \frac{1}{3}$ cps, a clear rotating skin sensation was obtained. But the stimulus on the right side lost its magnitude quickly because of the higher frequency, and, as indicated in Fig. 13-72, every time the sensation was located at the extreme right side the sensation became weaker and weaker, until after 9 sec of presentation time nothing more was felt on that side. On the left side the sensation still appeared and disappeared periodically, proving that the stimulus that was not felt was still able to inhibit the other. Of interest in this connection is the situation after 10.5 sec, when two stimuli were presented to the fingers but nothing was felt. This seems to indicate that adaptation and fatigue may occur at higher levels also.

The rotating skin sensations are of considerable interest because they seem to make possible the investigation of problems of fatigue and adaptation. It is generally believed that fatigue and adaptation are produced mainly in the end organs, and the higher centers show less change. The rotating skin sensation between the fingers of the two hands represents an inhibition of one side by the neural action of the other side. For example, if the right-hand finger adapts and the fatigue and adaptation are peripheral, the nervous action on the right side will no longer be able to inhibit the stimulus on the left side, and the whole sensation will travel to the left side, because on the right side the sensation is weakened. But if the adaptation is produced partly at a

The two finger tips are not the best places to carry out this experiment. In addition to the sensation on the surface of the skin immediately beneath the vibrator tip, there is a diffuse sensation caused by action on the tendons of the finger. This tendinous sensation fatigues at a slower rate. Therefore the skin sensations only were perceived in the immediate neighborhood of the vibrator tips. But on areas such as the chest the tendons and muscles do not disturb the sensations, and there is a periodic absence of sensation, as shown in Fig. 13-72. Naturally the slightest lateral movement of the skin may destroy the phenomenon, for unadapted skin may come under the vibrator. The experiment is a delicate one.

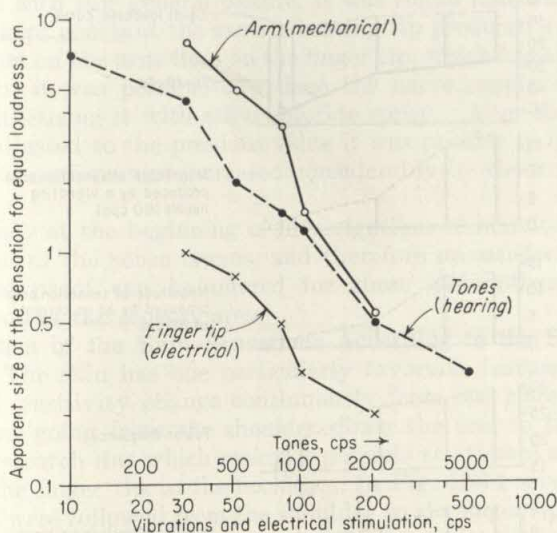


FIG. 13-73. Comparison of the apparent size of sensations as a function of frequency, for tones, mechanical vibrations, and electrical stimulation.

Apparent Size of the Sensation. During the study of the rotating skin sensations, it was observed that a phase change between stimuli on the two fingers not only changed the position of the area of sensation, but affected also to a large extent the size of the sensory area. This happened despite the fact that the physical distribution of the vibrations on the tip of the fingers did not change. If a single area on the skin was stimulated, it usually was found that the apparent size of the sensation decreased definitely if the stimulation was of short duration. As demonstrated earlier, a frame pressed against the lower arm with constant pressure was felt in general along the full extent of its contact with the skin. But if the frame was struck sharply, then only a sensation of about 1 cm length was felt, even when the length of the frame was more than 13 cm.

A closely similar situation holds for hearing. The sound image of a 50-cps tone seems at a certain loudness to fill up the whole head. But

when the frequency rises the sound image becomes smaller and smaller, as can be seen in the dotted curve of Fig. 13-73. The same holds for clicks.

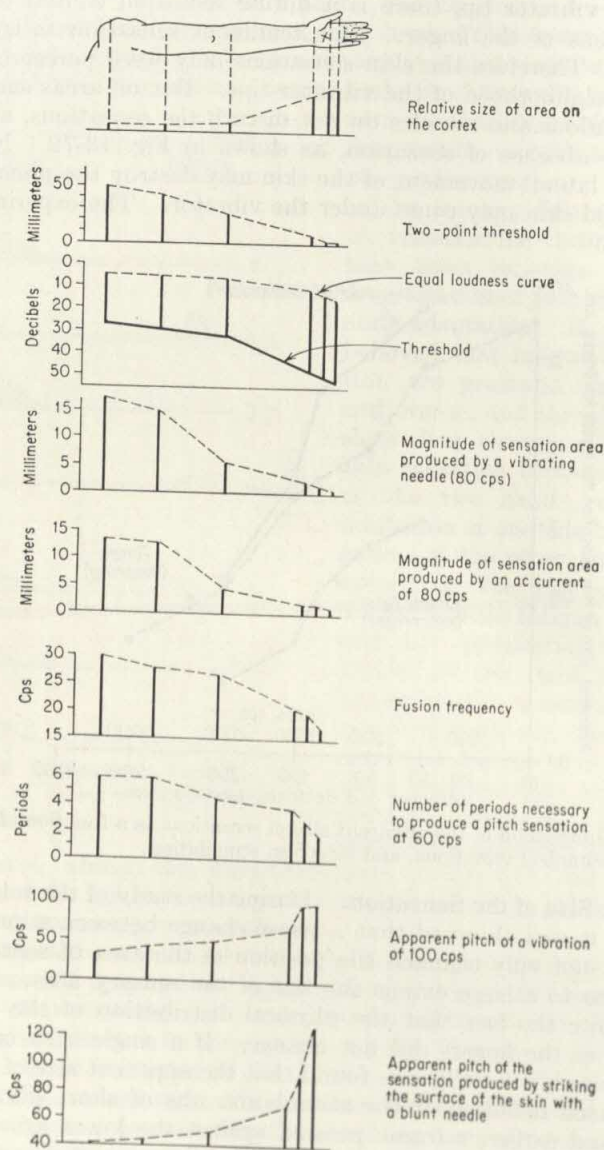


FIG. 13-74. Effects of bodily location on skin sensitivity.

Low-frequency clicks seem to have a large size, but sharp clicks have a sound image of only a few millimeters, especially if repeated in a series.

Not only for mechanical vibrations of the skin and in hearing does the apparent size decrease with increasing frequency and constant loudness,

but also for electrical stimulation of the finger tip, as shown in Fig. 13-73. Furthermore, the slopes of the curves for mechanical and electrical stimulation and for hearing are closely similar.

Because the sensory area becomes sharpened up relative to the spread of the stimulus when there is a sudden change in the stimulus, it is suggested that in Fig. 13-57 the lateral nerve branches in the plexus and the higher levels are active and produce inhibitions only when the nerve tracts are stimulated suddenly. During a long-lasting steady stimulus, the lateral nerve connections become less active and the extent of the sensation is shown mainly by the ascending nerve tracts. This seems to be a general feature of nervous tissue.

In accord with this general picture, it was found that when the magnitude was kept constant the same vibrating tip produced a much larger skin sensation on the arm than on the finger tip, which has a larger nerve supply. But it was possible to reduce the nerve supply of the finger tip by anesthetizing it with ethyl chloride spray. After the magnitude had been adjusted to the previous value it was possible to note that the size of the sensations was increased considerably by the freezing of the finger.

We are only at the beginning of investigations of inhibitory reactions in the plexus of the sense organs, and therefore no satisfactory electrophysiological proof can be offered for these assumptions about the sharpening up of the sensory area.

Modification of the Skin Sensations According to the Sensitivity of the Skin. The skin has one particularly favorable feature. Its nerve supply and sensitivity change continuously from one place to another. For instance, going from the shoulder down the arm to the finger tip we have a research line which makes it possible to attempt an extrapolation from the finger tip to the cochlea. In Fig. 13-74 several different phenomena were followed from the shoulder to the finger tip of the same observer to discover how an increase in the sensitivity of the skin, which in anatomical terms means a larger nerve supply, causes a change in the magnitude of different phenomena. The legends in Fig. 13-74 speak for themselves, and no further description is necessary. It should be mentioned only that, in addition to the line from the shoulder to the tip of the finger, there are lines of the same kind on other parts of the skin, and measurements on these parts show much the same characteristics as those found in Fig. 13-74.

FUNNELING IN THE NERVOUS SYSTEM AND ITS ROLE IN LOUDNESS AND SENSORY INTENSITY ON THE SKIN*

The relation between the subjective intensity of a vibration on the skin and the physical amplitude of the vibration is different for the different parts of the skin, for example, the finger tip and the shoulder. The reason for this is that the sensation of vibratory "loudness" is a complex interaction of summation and inhibition along the stimulated

* Article 82 as listed in the Author's Bibliography. Published in 1958.

skin surface. Both summation and inhibition vary with the amplitude of the vibration, the distance between the stimulated areas, the slope of the spatial distribution of the stimulus along the surface of the skin, its time pattern, and the density of the innervation. These relations have been described as variations in "funneling action" of the nervous tissues in the hope that this terminology will lead to a better understanding of the various phenomena.

A series of experiments was designed to establish rules for the estimation of the funneling action. For this purpose (1) the vibratory loudness produced by a point vibrator was compared with the "loudness" produced by stimulation of a large area of the skin (which may serve to explain why the curves of equal loudness for pure tones in hearing are compressed at the low frequencies); (2) the difference limen for amplitude variations was investigated under different conditions; (3) the lateral spread of the skin sensations was determined; and (4) all these phenomena were compared with analogous sensations in hearing. Through the concept of funneling, rotating skin sensations are brought into close relation with rotating tones, and Mach's law of contrast in vision with a similar phenomenon of the "funneling" action observed on the skin. Finally, it is demonstrated by experiments that once a funneling action is established on the skin, there is a certain period of time during which it inhibits all other sensation, exactly as in hearing. It is similar to the refractory period of the nerves. These refractory times are considerably longer when the funneling action takes place at the higher levels of the brain.

Histological sections of the nervous system show a strong resemblance to a telephone network. The transmission pathways of the nervous system, for instance, and the cross section of the auditory nerve with its nerve fibers look almost like telephone cables. The nerve centers with their branching fibers are similar to a switchboard. It was this analogy that probably suggested the theory that every stimulated end organ transmits electrical pulses along a predetermined pathway to the cortex, so that on the cortex there appears a map of the stimulated end organs. Today we think that this picture may be correct in small sections of the nervous system, but, in general, neurological evidence does not support it.

One of the difficulties with the electrical analogy is that the nervous system is not a passive system that comes to rest when there is no stimulus. On the contrary, in the nervous system there is continuous activity in the background, which may be increased or decreased when a stimulus is applied. Sometimes, the stimulus acts mainly by changing the normal activity. Naturally this makes the analogy with a telephone system forced.

Another difference between the nervous system and the analog is the fact that, as neurohistology has progressed, more and more connecting pathways have been found between the different nerve centers. Naturally if every center is connected to every other center, histology will not help us to investigate neural functions. It seems as important today

to map where connections do not exist between centers as to find new connections. But, unfortunately, negative statements are much more difficult to make than positive ones, and therefore histology does not help us to limit our attention to certain pathways.

Thus we are left with a picture in which the sensory nervous system is represented by interconnected lumps of more or less homogeneous tissue, in which the pathway of the neural action is only vaguely defined and may change considerably with the lateral distribution of the stimulus and with several other factors. In these interconnected lumps, the adjacent parts of a stimulated area may interact with each other in at least three different ways. (1) Summation results when the neural activity produced by one stimulus is increased by simultaneously presenting a second stimulus on an adjacent area of the sense organ. Subliminal stimuli can be brought above threshold if similar subliminal stimuli are presented on adjacent sections. (2) In inhibition just the opposite occurs, and a second stimulus may diminish the activity produced by the first one, or the two stimuli may cancel each other out. Clear inhibitory mechanisms are the antagonistic muscles, in which one is always completely relaxed when the other is in action, as for instance, the extensor and flexor muscles of the arm. Another simple inhibitory phenomenon in the sense organs is the rivalry of the visual fields of the two eyes. If one eye is presented with horizontal stripes and the other with vertical stripes and we look at the two fields simultaneously, we may see an alternation of the stripes, or one section of the visual field may be filled with horizontal and the other with vertical stripes. These are examples of pure inhibition. (3) In the phenomenon which will here be called "funneling," summation and inhibition occur simultaneously in the sense organs. This effect was discussed in the preceding section in connection with a multiple-vibrator experiment. Five vibrators were placed along a line on the skin of the forearm 2 cm apart. The amplitudes of the vibrations were adjusted so that they felt equally intense when presented separately. Their frequency was increased in one-octave steps from the upper arm to the forearm. When all five vibrators vibrated simultaneously, in spite of their different frequencies only the one vibrator in the middle was felt with its subjective frequency corresponding to its physical frequency. The "pitch" sensation of the other vibrators was completely inhibited, and they disappeared from the picture. But not so for the sensation of intensity of the other vibrators. The vibrators whose "pitch" was inhibited still contributed to the "loudness" of the vibrator in the middle. This sort of neural interaction may be called "funneling." It is relatively easy to observe along the surface of the skin because the vibrators on the sides shift their apparent locus to the middle and in this way increase the "loudness" of the vibrator in the middle. Because of this lateral displacement, funneling is different from pure inhibition in which one of the sensations is simply suppressed. It has some features in common with the concept of convergence, which Sherrington introduced and described in connection with the action of the spinal cord.

Another instance of funneling is found in directional hearing. When a sound strikes the two ears, the difference between the times of incidence at the two ears determines the apparent location of the sound source. If the time difference is large enough, the sound source is located in one ear and nothing seems to be heard in the other ear. In spite of this fact the apparently inactive ear is not inhibited in the sense in which inhibition is understood in antagonistic muscle groups or in the rivalry of visual fields, because inserting an earplug into the seemingly inhibited ear causes a definite decrease in the loudness of the sound heard by the other ear.

It may be that the types of neural interaction—namely, summation, inhibition, and funneling—occur at different levels along the neural pathway to the cortex. Perhaps at least four different levels can be discriminated. (1) There are many lateral nerve fibers running along the surface of the basilar membrane and the skin. These probably produce interaction at the level of the end organs. (2) Directional hearing between the two ears is an interaction on a higher level, as is the displacement of the vibratory sensation from a finger of the left hand to the right hand by a time delay between presentations of the stimuli. This interaction occurs only if the stimuli have some features in common. (3) Inhibition can occur even when the stimuli are very different. For instance, at a social gathering when several people are talking simultaneously, we can concentrate our attention on a single speaker and suppress all the others to a certain degree. This is probably inhibition at the cortical level, because we are really suppressing words and sentences and not just simple sound stimuli. (4) An even higher level may produce funneling and inhibitory effects when sound patterns touch off an activity that is stored in memory, as in the case of the miller who wakes up when the grinding noise of the mill stops. Changes in cortical electrical activity can be demonstrated for this kind of action (Galambos). It is probable that in most of hearing and for most skin sensations, there are interactions at all the different levels simultaneously.

The present section describes several experiments on the interaction of the skin and compares them with similar phenomena in hearing. An attempt is made to bring them under one common heading by describing them in terms of a funneling action of the sensory nervous system. There are so many kinds of summation, inhibition, and funneling phenomena that it is difficult to foresee at the moment how successful such a description will be. Fortunately, the analogy between the skin and the ear can be extended to the retina, and, as shown in the work of Hartline, Kufner, and Barlow, and of Barlow, Fitzhugh, and Kufner, some of the visual phenomena are strikingly similar. It seems certain that knowledge of the retina will greatly aid in an understanding of some of the neural processes in hearing, and that measurements on the three sense organs will complement one another. This is important because certain measurements are more easily made for the eye than for the skin or the ear.

One difficulty with measurements on the skin is that there are as many

types of skins as there are types of faces. The individual differences are large. A second difficulty is that the pulse can set up a disturbing internal noise level. Especially on the finger, the pulse may produce movements that are difficult to distinguish from the low-frequency movements produced by a vibrator. In spite of these difficulties, however, it has been possible to establish some generalizations concerning the interaction between adjacent parts of the skin during vibratory stimulation. It is possible to bring the relative variations in vibratory magnitude, the threshold, and the apparent size of the stimulus under a common point of view for the different types of stimulus distributions along the surface of the skin.

In summary, it is found that the funneling action becomes larger when (1) the stimulated area on the skin is large, (2) the density of the nerve supply is large, (3) the slope of the distribution of vibratory amplitudes along the skin is steep, (4) the stimulus is short, and (5) there is a time delay between the vibrations. The funneling becomes smaller when white noise is superimposed on the stimulus.

If the funneling action is large, then (1) the threshold is relatively low, (2) the difference limen is relatively large, and (3) the apparent size of the sensation is relatively small.

Definition of a Good Subject. Because judgments of apparent intensity are subjective observations and show great variability, we may begin with the question, how can we discriminate between good and poor observations? Or should we have no discrimination at all as to the subjects and their statements?

When continuous vibratory stimuli are presented on the skin the subject can differentiate several attributes: (1) the frequency of the vibration, which is analogous to pitch in hearing, (2) the subjective magnitude of the sensation, which has many features in common with loudness in hearing, and (3) the sensation of the lateral spread along the surface of the skin, which corresponds to the volume of the sound in hearing. These three attributes will be referred to as vibratory "pitch," or pitch; vibratory magnitude, or loudness; and lateral spread.

The same surface of the vibrator touching the skin may produce sensations of lateral spread very different in size, depending upon the nature of the stimulating vibration. In general, low-frequency sinusoidal vibrations spread out along the surface of the skin, whereas a series of clicks is felt on only a small area. This situation is illustrated in Fig. 13-75.

An untrained subject was presented briefly with two vibratory patterns, a series of clicks and a sinusoidal vibration, and was asked to adjust

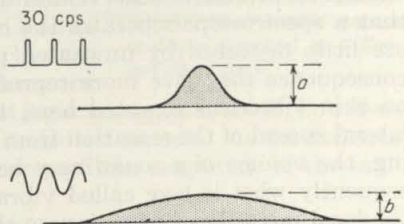


FIG. 13-75. Distribution of the local sensory magnitude along the surface of the skin for the same frame vibrating (a) in the form of clicks and (b) with a sinusoidal amplitude.

them to equal vibratory magnitude. He was then asked to make a drawing of the distribution of the sensory magnitude along the surface of the skin, repeating the stimuli as many times as necessary to determine the shape of the distribution. For two vibrations applied to the forearm at a frequency of 30 cps, the drawings corresponded to the distributions shown in Fig. 13-75. The maximal local intensity of sensation was about one-third higher for the clicks *a* than for the sinusoidal vibrations *b* when they seemed equally loud. This situation raises a question for all subjects, whether the vibratory magnitude as a whole is determined by the area of distribution of the local intensity of sensation or by the maximum.

Continued observations taught the subject to discriminate between the different attributes of the sensations produced by the vibrator. The experiments showed that after some training most subjects had difficulty in making an over-all, prompt judgment of vibratory magnitude, because as a consequence of the training they always observed the local intensity of sensation. When they had reached this stage of training, the adjustment of two vibrations to equal loudness, as in Fig. 13-75, meant for them an adjustment for equal maximal local intensity of sensation ($a = b$) and a complete ignoring of the lateral spread of the sensations. A good subject might be defined as a person who is able to separate the various attributes of the stimulus from each other well enough to be able to observe and describe them separately—in the way that a spectroscope separates the colors of white light. Good subjects are little disturbed by unwanted phenomena, such as noise, and as a consequence they give more reproducible results. In the observations on skin vibrations reported here, the effort was made to separate the lateral spread of the sensation from the local maximum—just as in hearing, the volume of a sound may be separated from its loudness. Consequently what is here called vibratory magnitude is the maximum of the local intensity of sensation on the surface of the skin.

In carrying out research with the aim of establishing sensory relations which can later be correlated with physiological phenomena, it is preferable to work with a small number of analytically minded subjects. At the other extreme, there are mass observations, such as those carried out at a fair. There the observation time is short enough that even with untrained subjects it is possible to produce judgments that are often reproducible. But these observations may differ considerably from the observations of an analytical subject. For instance, in mass comparisons of the loudness of a noise with the loudness of a low-frequency tone, the results are often affected by the apparent size of the sound image, the sound with the larger image being judged the louder. To an untrained subject size or volume seems to take precedence over the other attributes. The writer's conception of a poor subject is a person who has worked long enough in a laboratory to have lost his ability to make naïve observations but has not been able to achieve a really analytical stage.

Interaction between Two-point Stimuli. Beginning with the simplest conditions, a comparison was first made between the effects of increasing

the amplitude on the vibratory magnitude produced by two vibrating points and that produced by one side of a vibrating frame. Both the frame and the two points stimulated the inner side of the forearm. For the two-point measurements, two small points were attached to the frame. The distance between the points could be varied (see Fig. 13-76). The frame was made of hollow tubes, so that it would be as light as possible, and the tubes were attached to a large electrodynamic driving unit. The resonance frequency was adjusted high enough, and the damping made as large as possible, so as to produce an equal frequency response and make the vibratory amplitudes of the frame independent of the load produced by its contact with the skin.

Figure 13-77 compares the relation of vibratory magnitude to amplitude for the two points at three different distances, and for the frame. The abscissa represents the vibratory amplitudes of the two points in decibels above threshold, whereas the ordinate is the vibratory amplitude of the frame in decibels relative to an arbitrary zero point. Close to threshold the magnitude produced by the points rises much more rapidly than the "loudness" produced by the frame. At higher magnitude levels, however, the steep slope of the two-point magnitude flattens out. As the distance between the two vibrating points is increased the magnitude of the two-

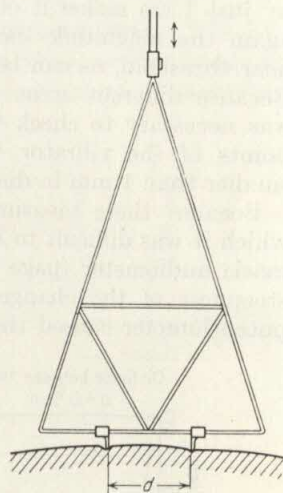


FIG. 13-76. Frame made of tubes used to stimulate a longitudinal section of the skin. For two-point stimulation, two small points could be attached at different distances d .

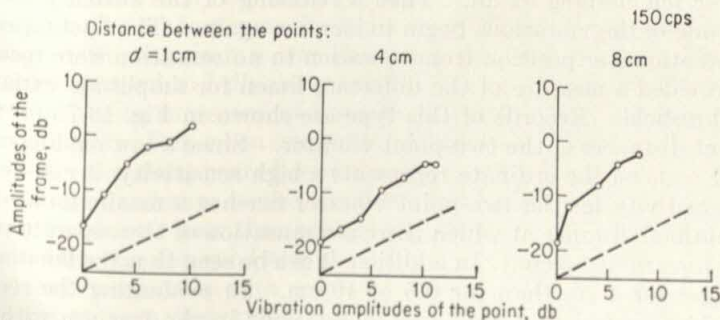


FIG. 13-77. A comparison of the vibrating magnitudes produced by two points and by a frame. Three separations of the points were used. The amplitudes are in decibels above threshold. The dashed lines represent the slope that would be obtained if the two forms of stimulation were equal.

point sensation continues to increase, but the rise is not as steep near threshold, and, when the distance between the points is 4 cm, the magnitude of the two points and the frame increases in almost the same way.

This is about the distance at which, on the inside of the forearm, two points cannot be separated and are felt as one. Increasing the distance by just 1 cm makes it obvious that there are two separate stimuli, and again the magnitude increase for the two points shows the steep rise near threshold, as can be seen in the right-hand drawing of Fig. 13-77. Because different areas on the skin may have different sensitivity, it was necessary to check the sensitivity along the line between the two points of the vibrator. In addition, the vibrator tips could not be smaller than 1 mm in diameter.

Because these measurements required a good deal of time during which it was difficult to keep the vibrator tips exactly in place, an automatic audiometer (page 81) was used to advantage in determining the steepness of the changes in vibratory magnitude near threshold. A potentiometer caused the vibratory amplitude to increase continuously

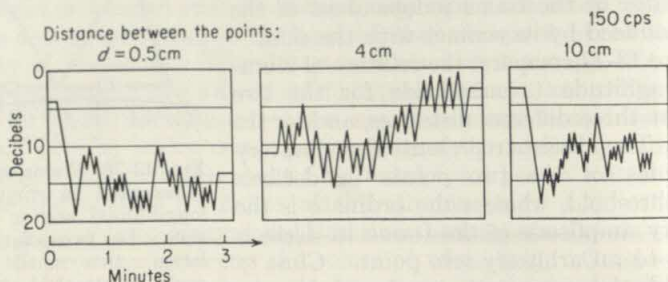


FIG. 13-78. Threshold measurements with the automatic audiometer.

until the observer felt the vibration. The moment he felt it, he pressed a microswitch that reversed the direction of the potentiometer and caused the amplitude to start decreasing. This change continued until the observer felt nothing at all. Then a releasing of the switch made the amplitude of the vibrations begin to increase again. The fluctuations of the potentiometer position from sensation to no sensation were recorded and provided a measure of the difference limen for amplitude variations near threshold. Records of this type are shown in Fig. 13-78 for three different distances of the two-point vibrator. Since a low reading on the decibel scale on the ordinate represents a high sensitivity, it can be seen that sensitivity for the two-point vibrator reaches a maximum at 4 cm. The minimal distance at which there is a sensation of two separate points on the forearm is 4.5 cm. In addition, it can be seen that the fluctuations are larger for 4 cm than for 0.5 or 10 cm. In evaluating the records, it should be noted that the large fluctuations in the tracings with long periods of stimulation are a consequence of periodic variations in skin sensitivity produced by pulse, breathing, and small displacements of the vibrators.

In summing up these two-point experiments it may be said that the addition of a second stimulating point within a certain radius of "action" increases the sensitivity for vibrations through neural summation. At the same time, a given amplitude variation near threshold changes the

vibratory magnitude less for two-point stimulation than for stimulation with a single point. For higher loudness levels, however, there is no difference.

Magnitude Curves and the Size of the Stimulated Area. The two-point magnitude curves discussed in the preceding section suggested that there is a radius of action for the summation of vibratory magnitude on the skin which has about the same size as the liminal separation of two simultaneously stimulated points. The question is, how does the summation take place if it works not only along a line but over a whole surface? To investigate this the vibratory magnitude produced by a point vibrator whose tip was 1 mm in diameter was matched to the magnitude produced by a round, flat frame with a diameter of 7.5 cm. Both vibrators are shown in Fig. 13-79. The frame consisted of brass tubes, 1.5 mm in diameter, soldered together in the manner shown. The tip of the point vibrator was placed in the center of the inner ring of the frame in order to eliminate as much as possible the variations in skin sensitivity along the forearm. The stimulation found most successful for loudness matching was to let the tip vibrate alone once and then to vibrate the frame and tip with the same amplitude, so that together they formed a vibrating network. As the vibrations of the tubes lying flat on the skin spread out laterally a few millimeters, the whole surface is set in vibration in the same phase, as can be checked by stroboscopic observations.

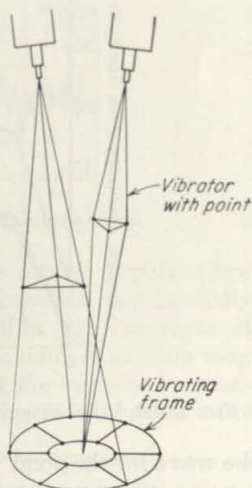


FIG. 13-79. Apparatus for the study of areal effects.

Curves of vibratory magnitude for three different subjects are shown in Fig. 13-80. Again it is true that when the vibratory amplitude of the point is increased to 5 db above threshold, the vibratory amplitude of the frame has to be increased at least 20 db to keep the sensations of magnitude equal. But when the point vibrated at 25 db above threshold, this difference disappeared, and the frame and the point reacted in the same way to a change in the vibratory amplitude. The steepness of the rise in "loudness" near threshold for the point relative to the large vibrating surface was observed also in measurements of the difference limen for vibratory magnitude with the automatic audiometer. The difference limen is at least four times larger for the frame than for the tip. In every case observed, each increase in the size of the stimulated area produced an improvement in sensitivity and at the same time gave an increase in the difference limen near threshold. Even increasing the spread of the waves along the surface of the skin by sticking adhesive tape on the skin (as shown in Fig. 13-81) increased the difference limen noticeably. Figure 13-82 shows the fluctuations of the audiometer record for one edge of a vibrating frame touching first the normal skin

surface and then the adhesive tape stuck to the skin. The displacements of the adhesive tape produced mainly shearing forces in the skin, which seem to be the stimulating forces in the deformations of the skin.

The magnitude curves obtained in the frequency range between 50 and 400 cps have the same shape as those shown in Fig. 13-80. Below 50 cps

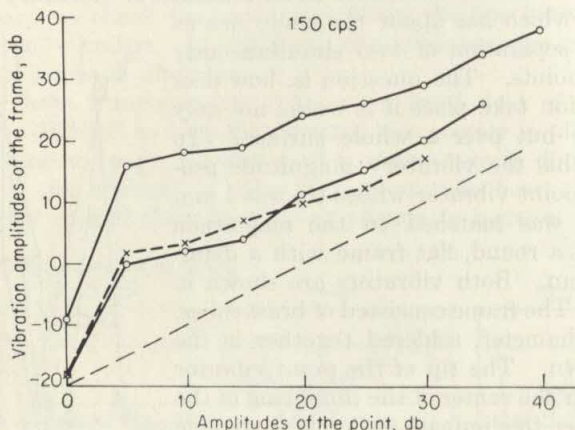


FIG. 13-80. Equal-magnitude curves for a point vibrator and an areal stimulator.

the wave for the point vibrator spreads far out, which indicates that even a point vibrator stimulates a relatively large area. But the magnitude curves may vary considerably from one place on the skin to another—partly because of mechanical differences in the skin, partly because of differences in the density of the nerve supply of the skin. For precise

measurements it should be taken into account that every section of the skin has a different curve. This variation was found in an earlier study in curves of equal magnitude for places on the skin from the shoulder down to the finger tip (page 566). But changes in the shape of the magnitude curve are usually very large when the stimulated area is increased from the size of the tip of a needle to a line a few centimeters long.

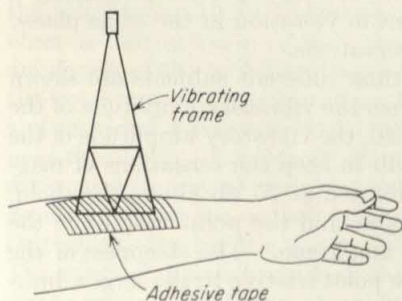


FIG. 13-81. Method of applying adhesive tape to the skin.

However, if the vibrator is increased in length from a few centimeters to the full length of the forearm, the magnitude curve changes little, and it approaches asymptotically a magnitude curve corresponding to an extremely large surface with a large number of sensory cells. Because of the close relation between the skin and the ear, it is therefore not surprising that, if we compare the vibratory magnitude curve of the finger tip, which is the most sensitive section of the skin and has the

largest number of nerve cells, with the loudness curve produced in the ear by a low-frequency tone, we find their slopes not too different from each other (Stevens, Carton, and Shickmann, and page 249).

These magnitude measurements lead to one further speculation. It was found that sensitivity improves as the surface of stimulation is increased, which means increasing the number of the stimulated cells.

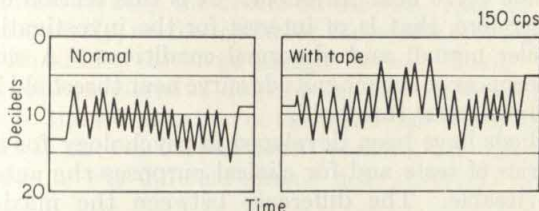


FIG. 13-82. The effects of adhesive tape on the difference limen.

It is known that the sense organs of most insects consist of only a few sensory cells. But the number of sensory cells increases continuously from insects to fishes, reptiles, and mammals, until in man the organ of Corti has about 30,000 cells. This increase in the number of cells may serve as one way of increasing sensitivity, and yet the increase in sensitivity may, according to the measurements in Fig. 13-80, be no more than 10 or 20 db. Certainly the lower thresholds produced by summation are much more stable and reliable than the threshold of an organ of only a few cells.

As the small increase in sensitivity that accompanies the increase in number of the sensory cells does not seem to justify 30,000 cells in the organ of Corti, it seemed desirable to investigate whether the signal-to-noise ratio is better in an organ containing a large number of cells. For this purpose the frame was applied to the forearm first with a sinusoidal vibration of 150 cps and with a distribution of the magnitude of the sensation along the skin as shown in the upper drawing of Fig. 13-83.

Stimulation with a slightly more intense random vibration (white noise) gave the distribution shown in the second drawing. When both stimuli were presented together, the sensory magnitude for both increased a little and spread out laterally. The same sequence repeated with a vibrating tip gave exactly the same results. The larger frame in no way improved the discrimination between the sinusoidal vibrations and the random vibrations. A frame was even made consisting of six different sections,

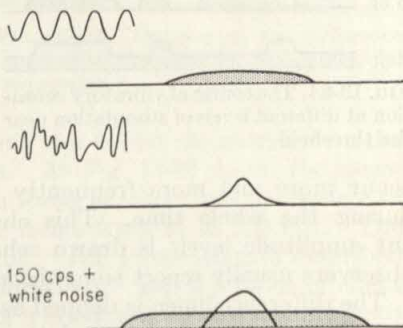


FIG. 13-83. Effects of the type of signal on the distribution of sensation. The upper sketch represents a sinusoidal vibration of 150 cps, the next one a white noise, and the lower one a combination of the two.

each driven by a different random generator to simulate Brownian movements on the skin and the organ of Corti, but this out-of-phase vibration produced exactly the same sensations as the vibrations of a single generator.

Difference Limen for Amplitude Changes. Variations in the stimulated area or in the number of stimulated end cells modify mainly the steepness of the magnitude curve near threshold. It is this section of the magnitude curve, therefore, that is of interest for the investigation of neural interaction under normal and abnormal conditions. A simple way to measure the steepness of the magnitude curve near threshold is to measure the difference limen near threshold.

Several methods have been developed in psychology for this purpose. For a large series of tests and for clinical purposes the automatic audiometer is serviceable. The difference between the maxima and the minima in the tracing of the record, expressed in decibels, gives a measure

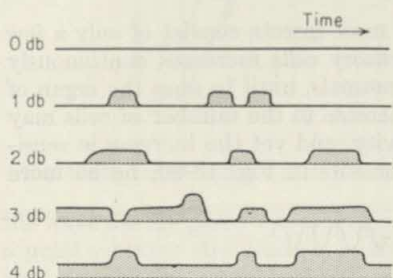


FIG. 13-84. The course of vibratory sensation at different levels of stimulation near the threshold.

that is here called the difference limen. The values obtained are in general about twice as large as those found with the usual psychophysical methods, but this is only a consequence of the definition of the difference limen. As indicated earlier,* if the vibratory amplitude increases continuously and automatically from a value below the threshold, at first nothing is felt, as shown on the upper line in Fig. 13-84. As time goes by sensations occur for short intervals, and they

occur more and more frequently until finally the sensation is present during the whole time. This change in the time pattern for different amplitude levels is drawn schematically in Fig. 13-84. Analytical observers usually report some discrete sensory intensities.

The difference limen is defined as the difference between the amplitude for which nothing is felt and the amplitude at which the sensation is present half the time, corresponding approximately to the level of 2 db in Fig. 13-84.

As amplitude on the automatic audiometer decreases, most observers record the point where nothing is felt, and, as the amplitude increases, the point where the sensation just seems to stay on continuously, and this corresponds to about the 4-db level in Fig. 13-84. Hence the difference limen recorded with the audiometer is approximately twice the size of the difference limen as usually determined in psychology. Because the measurements described here were made with the automatic audiometer, they will be expressed in terms of the larger value.

The continuous recording made it possible to discriminate the fluctuations in the difference limen that resulted from accidental changes in the

* See Art. 50 in the Author's Bibliography.

sensitivity of the skin. This effect is shown in Fig. 13-85 where an attempt was made to determine approximately the smallest obtainable difference limen. The measurements were made on the chest, with the edge of the frame stimulating the left side and a needle tip stimulating the right side. When the needle tip touched a sensitive spot on the skin, the difference limen went down to 1 db by the audiometric measurement. But it was difficult to keep the needle on the same spot for any length of time, and consequently, on the record for the needle four separate sections can be seen, with sudden threshold changes between them. These sudden changes were not considered in determining the difference limen.

Going back to the examination of the difference limen as a function of various factors it should be mentioned that on the skin as well as in hearing, the size of the difference limen near threshold did not depend

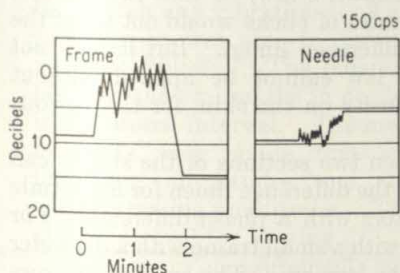


FIG. 13-85. The just-noticeable amplitude variations for a frame and for a needle acting on a sensitive spot.

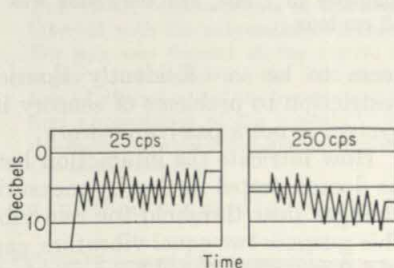


FIG. 13-86. The size of the difference limen near threshold for two sinusoidal frequencies.

noticeably on the frequency. In hearing this is best recognized from the equal-loudness contours for pure tones. As Fig. 13-86 shows, for measurements made with the frame on the forearm, there was no change in the size of the limen in the frequency range from 25 to 250 cps. The same holds for stimulation with a point. The measurements described above were all made with sinusoidal vibrations. But if a series of clicks was used, produced by the discharge of a condenser at the rate of about two per second, most of the phenomena changed considerably. For instance, when the edge of the frame, 13 cm in length, stimulated the skin of the arm with a sinusoidal vibration, the sensation spread out laterally about 10 cm, depending on the frequency and the vibratory magnitude. But if short clicks were used, the lateral spread was often less than 1 cm. As a consequence of this phenomenon the difference limen for the sensation of distance on the skin of the arm was found to be almost twice as large for sinusoidal vibrations as for clicks.

Because the lateral spread for the click is so small and all the sensations on the edge of a large stimulated area are suppressed, it is not surprising that the difference limen for amplitude changes for the click is almost independent of the size of the stimulated area, in complete contrast to the situation for sinusoidal vibrations. Figure 13-87 shows the audiometric records for a series of clicks applied to the arm, one with the edge of the

frame and the other with a needle 1 mm in diameter. The difference limen is only a little larger for the frame than for the needle. Stimulation with clicks changes the whole slope of the magnitude curve as obtained

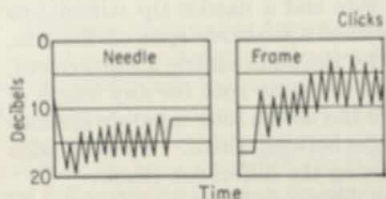


FIG. 13-87. Relation between the size of the stimulated area and the difference limen for clicks. The needle had a diameter of 1 mm, and the frame was 13 cm long.

by matching the vibratory magnitude of a tip with that of a frame. This fact is interesting because according to Fig. 13-86 the difference limen for sinusoidal vibrations does not change appreciably with frequency for the frame or for the point vibrator. From this we would expect that combining different frequencies, according to Fourier's law, so that they form a series of clicks would not affect the difference limen. But it does not

seem to be so. Evidently Fourier's law cannot be applied without restriction to problems of sensory intensity on the skin, for the nervous system is not a passive network.

How intricate the interaction between two sections of the skin is can be demonstrated further by measuring the difference limen for amplitude changes near threshold for two vibrators with a phase difference. For this purpose two equal vibrators, each with a small frame with a diameter of 1.0 cm, were placed 8 cm apart on the forearm. The amplitudes were adjusted precisely to the threshold values, and they were both increased or decreased in the same way, depending on the potentiometer position on the audiometer. One of the vibrators was attached to a phase shifter, so that the relative phase between the two vibrators could be set at any value. It then turned out that when there was no phase difference the lateral spread of the sensation was very large and the difference limen was large also. But if there was a small phase difference and the sensation was localized completely to one side, the lateral spread became small and the difference limen perhaps twice as small. A small phase difference is enough to mask one vibrator and to produce a difference limen of the size that would be produced if the stimulated surface area were decreased from 10 to 1 cm. At threshold the sensitivity, however, is better if there is a phase difference and the vibrations are localized to one side. When there is a phase difference we have a spatial interaction with a time delay as a new element in it.

Atonal Interval for Vibratory Sensation and Hearing. There are two difference limens for amplitude variations: (1) the just-noticeable vibration, and (2) the amplitude at which not only is the vibration noticeable but its "pitch" can be determined as well. The difference between these two thresholds is called the atonal interval, because in this range there is a sensation but the "pitch" is indeterminate. The atonal interval for hearing has been determined for various frequencies (Harris and Meyers; Pollack). This atonal interval is even less specific than the difference limen for loudness because the sensation of pitch creeps in very

slowly. The magnitude of the atonal interval depends markedly on the method of observation. Nevertheless it is of interest because it shows a definite difference between hearing and the vibratory sense.

Observations were made on the skin with the automatic audiometer, which increased the vibratory amplitude of a small frame 1.8 cm in diameter from below threshold, at a speed of 0.7 db per sec. The subject touched the vibrator with his left thumb and made a mark on the audiometer record, as can be seen in Fig. 13-88, (1) when he first felt any vibration at all and (2) when he was able to discriminate the "pitch." The difference between the two marks in decibels is the atonal interval. The measurements were made first with increasing amplitudes and then with decreasing amplitudes. The same method was used to measure the atonal interval for hearing.

Of the many measurements made the only ones to be mentioned represent the change in the atonal interval when the presentation time of the

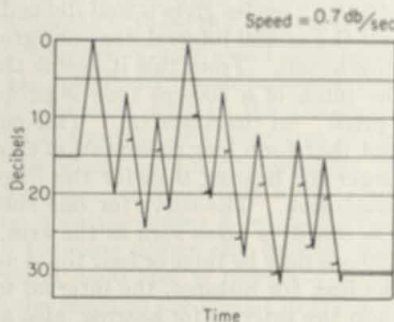


FIG. 13-88. Measurements of the atonal interval with the automatic audiometer. For any one descent of the curve, the upper mark represents the first perception of vibration and the lower mark the first appreciation of the "pitch." The distances between these marks represent the atonal interval.

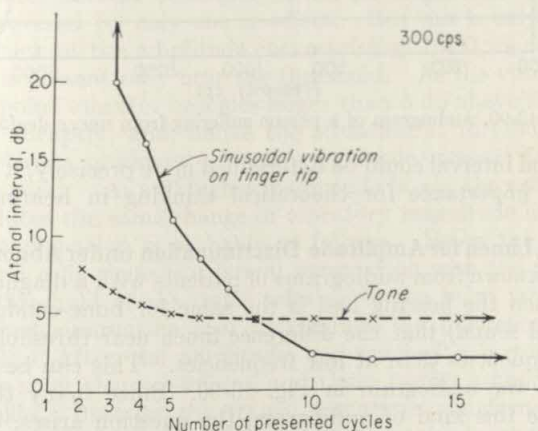


FIG. 13-89. Effects of the duration of stimulation on the atonal interval for tones and for vibrations on the skin.

vibration or the tone was shortened. These results are shown in Fig. 13-89. With the sinusoidal vibrations, the interval grew rapidly as the presentation time dropped below 10 cycles, and below 3 cycles confident judgments of pitch were no longer reported. These measurements were

made by stimulating the finger tip with 300 cps. The results are different for hearing, as can be seen from the dotted line in Fig. 13-89. Here as little as 2 cycles gives a well-defined sensation of pitch, as is well known, and the atonal interval does not grow smaller as the presentation time is lengthened. From this it seems that, in hearing, the discrimination of the pitch of a 300-cps tone is probably different from the sensation of "pitch" on the finger tip. This conclusion is further supported by the fact that for a long presentation time the atonal interval was found to be larger for hearing than for the finger tip. Several subjects reached this conclusion. The curve for one subject can be seen in Fig. 13-89. On less sensitive areas such as the arm, the atonal interval for vibrations at 300 cps may be three or four times as large as on the finger tip, whereas on the lips, for instance, the interval may be as much as five times smaller than the interval for hearing, also at 300 cps.

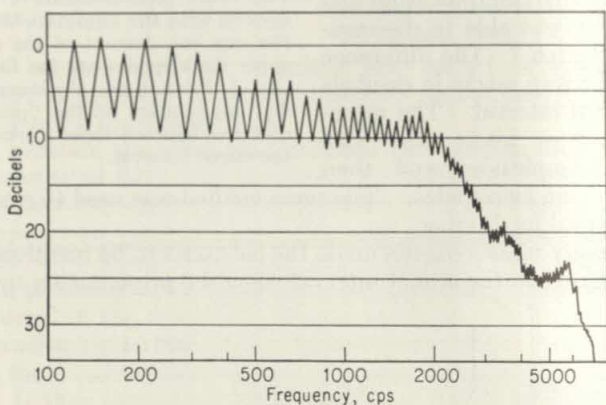


FIG. 13-90. Audiogram of a person suffering from nerve deafness.

If the atonal interval could be determined more precisely, it would have considerable importance for theoretical thinking in hearing and skin sensations.

Difference Limen for Amplitude Discrimination under Abnormal Conditions. It is known from audiograms of patients with a diagnosis of nerve deafness (when the hearing loss is the same for bone-conducted as for air-conducted sound) that the difference limen near threshold is smaller at higher frequencies than at low frequencies. This can be seen on the right side of the audiogram in Fig. 13-90. Since many thousands of patients have this kind of audiogram, the question arises, can we find any explanation for this condition?

We have learned from measurements on the skin that the difference limen near threshold becomes smaller and smaller as the size of the stimulated area is decreased. Automatically this would mean that a decrease in the number of stimulated end cells decreases the difference limen. This would fit in with the pathological picture that a disease reduces the number of active end cells. We have found further that

the decrease in the difference limen is relatively small when a large area starts to decrease, but it becomes pronounced when the stimulated area approaches the size of the tip of a needle. From this fact we would expect that a uniform decrease in the number of active end cells along the whole basilar membrane of the ear, produced by an inflammatory process of the labyrinth, would only decrease slightly the difference limen for the low frequencies, for with low frequencies a large area of the basilar membrane is stimulated. But it would have a greater effect on the difference limen for the higher frequencies, for which only a relatively small section of the basilar membrane near the stapes is set in motion by the tone. This seems to explain to some degree the finding that the difference limen, particularly around 4000 cps, is markedly small when there is nerve deafness, because the place on the basilar membrane that is stimulated by 4000 cps probably has a poorer nerve supply than other parts of the basilar membrane. By a poorer nerve supply is meant poorer lateral branching, because this point is on the border line between two separate nerve trunks going to the basilar membrane.

More difficult to answer is the question, why does a decrease in the number of active end cells diminish the difference limen? The writer's impression is that a single end organ has a relatively sharp onset, because throughout electrophysiology on-effects and off-effects play an important part, and these on-effects are stimulated when the vibratory amplitude reaches the threshold value. But if many end cells are present and they have lateral interconnections, then subliminal interaction takes place that distributes several on-effects within an amplitude range that was previously covered by only one on-effect. But this is only conjectural.

Looking back at the amplitude curves of Fig. 13-80 we can see that a steep slope is present only near the threshold. As the vibratory amplitude of the point vibrator becomes larger than 5 db above threshold, the slope drops abruptly, and, unlike the situation at threshold, the same amplitude change produces a larger magnitude increase for the frame than for the point. At still higher magnitude levels, the same amplitude change produces the same change in vibratory magnitude in both vibrators. The explanation is probably as follows. Below the threshold of the single end cells there is a lateral summation with the frame, which lowers the threshold of the frame relative to the point vibrator. It is this subliminal summation that determines the difference limen near the threshold. After the amplitude has reached a certain value, all the end cells start their on-effects, and there results a quick increase in the magnitude. Because the frame stimulates simultaneously many more end cells than the point vibrator, the magnitude increase is larger for the frame than for the point. For still larger vibratory amplitudes we have to take into account the fact that the mechanical spread of the waves for the point vibrator may stimulate larger sections of the skin, so that there is no longer the pronounced difference between the frame and the point stimulation that there was near the threshold.

We have an analogy in the hearing of pure tones if we assume that a low-frequency tone of about 50 cps stimulates a large area along the

basilar membrane like the frame, but that a tone above 3000 cps stimulates only a small area like the point vibrator. In hearing we would expect that near the threshold the curves of equal loudness would be farther apart for the low than for the high frequencies. But for medium loudness levels the curves of equal loudness are squeezed together at the low frequencies as compared with the higher frequencies, because a small change in amplitude at this level produces a large loudness change at the low frequencies. For still higher levels the curves of equal loudness should run parallel to one another over the whole frequency range. The curves of equal loudness for pure tones seem to show these trends (Stevens and Davis, page 124).

If the difference limen near threshold in Fig. 13-80 is a consequence of the subliminal summation through lateral neural interconnections, we can assume that the same holds for the ear. In nerve deafness this subliminal summation is apparently lost, and the threshold therefore becomes higher. The difference limen for amplitude changes near the threshold becomes small in accordance with the change in slope of the magnitude curves in Fig. 13-80. Probably nerve deafness causes a larger change in the difference limen near threshold than at higher loudness levels, and it is therefore more useful for diagnosis to measure the difference limen near the threshold than at higher levels.

In search for more information, an attempt was made to produce abnormal conditions on the skin and to investigate their effects on thresholds and difference limens. It is well known that either cold or warmth relieves pain and therefore puts some nerve endings out of action. Freezing the skin was earlier found to decrease the difference limen.*

But freezing the whole forearm with ethyl chloride spray was uncomfortable if maintained for a long time. Much more pleasant and stable conditions could be achieved by warming the arm with an infrared incandescent lamp. This relieves pain just as successfully as freezing and with much more lasting effect. The heated skin becomes less sensitive, as was noted by simply touching the skin. The

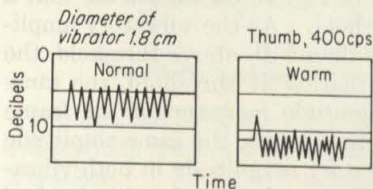


FIG. 13-91. Effects of warming the skin on the difference limen for amplitude.

change in the difference limen and the decrease in sensitivity of a heated thumb are shown in Fig. 13-91. As can be observed, the heating produced first a change in the difference limen and then a change in threshold. Sometimes there was a time lag of almost 2 min between the drop in the threshold and the change in the difference limen.

In order to demonstrate that heating the skin acts in the same manner as decreasing the nerve supply, the difference limen for distance was measured in the forearm first on normal skin and then at the same place when warmed up with the infrared lamp. The results, shown in Fig. 13-92, indicate that warming the skin increases the difference limen from

* See Art. 50 as listed in the Author's Bibliography.

about 2.5 to 4.0 cm—just the same as going from the forearm to the shoulder.

There was one interesting experience with these measurements. For most subjects heating or cooling the skin decreased the difference limen and made the threshold higher. It could be said, therefore, that the normal skin is adjusted so that the sensory nerves are maximally sensitive at a room temperature of approximately 65°F. But some subjects showed a definite lowering in threshold together with an in-

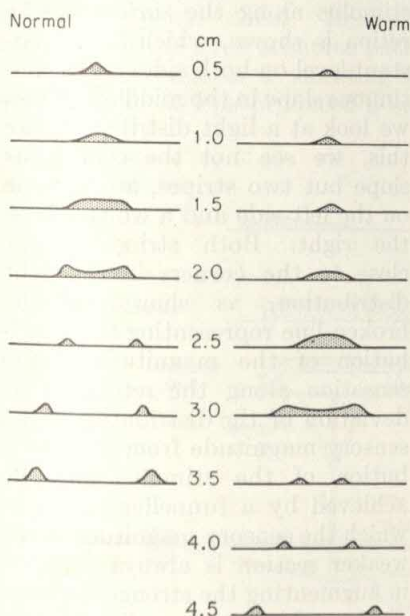


FIG. 13-92. Effects of warming the skin on the distance threshold.

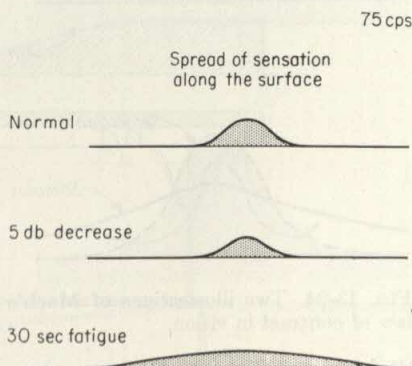


FIG. 13-93. The effects of fatigue on the distribution of magnitude on the skin.

crease in the size of the difference limen with slight heating, and a drop in sensitivity occurred only with a further increase in the heating. Their skin was apparently adjusted to a temperature above 65°F.

In addition to heat and cold, fatigue also changes the neural interaction along the surface of the skin, as Fig. 13-93 suggests. The top line of this figure shows the distribution pattern of the local sensory intensity for a vibrator with a diameter of 1.8 cm and operating at 75 cps. If the amplitude is decreased by 5 db, the lateral spread of the sensation becomes smaller, and the maximum of the sensation decreases also. But after 30 sec, when the skin is fatigued and the maximal sensation intensity has dropped the same amount as would be produced by an amplitude drop of 5 db, then it is found that the whole sensation spreads out laterally. This fact indicates that the whole neural lateral interaction was changed completely during the fatigue, and the funneling action of the nervous system was decreased.

Funneling Actions of the Vibratory Skin Sensations. As was mentioned in the introduction, we can bring the complex variations in the skin sensations into a common point of view if we describe them as a funneling action of the neural tissue. It is well known that if two sensations are produced side by side and one is much stronger than the other,

the weaker will be suppressed, but it may contribute to building up the stronger. In other words, there is a funneling toward the stronger sensation. This situation can be seen clearly in vision, where it is known as Mach's law of contrast. In the upper part of Fig. 13-94 a light

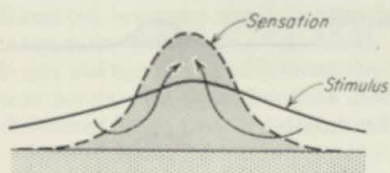
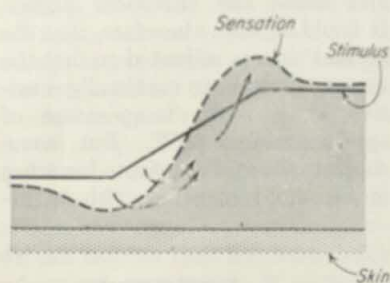


FIG. 13-94. Two illustrations of Mach's law of contrast in vision.

stimulus along the surface of the retina is shown, which has a constant level on both sides and a continuous slope in the middle. When we look at a light distribution like this, we see not the continuous slope but two stripes, a black one on the left side and a white one on the right. Both stripes appear close to the corners in the light distribution, as shown by the broken line representing the distribution of the magnitude of the sensation along the retina. This deviation of the distribution of the sensory magnitude from the distribution of the stimulus may be achieved by a funneling action in which the sensory magnitude of the weaker section is always depleted in augmenting the stronger section.

Stripes are formed because there is a certain action radius in this funneling procedure.

The lower drawing in Fig. 13-94 shows how, as a consequence of the funneling, a distribution of the light stimulus with a relatively flat maximum is transformed into a distribution of sensation with a much sharper maximum. This sharpening of a stimulus with a flat maximum is highly important in the localization of stimuli.

It is easy to demonstrate the validity of Mach's law for steady pressure on the skin by showing that the maximum of the sensation is localized near the maximal curvatures in the stimulus distribution (see page 419). In order to show the same thing for the vibrations on the skin, use was made of the arrangement illustrated in Fig. 13-95. The surface of the arm touched the edge of a plastic sheet which consisted of three rigid sections linked together at two points, *a* and *b*. The two end sections were each connected to a rod that rotated around point *c*. The other end of the rod was set in vibration by a large electrodynamic driving unit. Since the left-hand section of the plastic sheet was closer to the rotating point, its vibratory amplitudes were one-third as large as the amplitudes on the right side, and the distribution of the stimulus was like that shown in the figure. Vibrations of 100 cps were used, and if the forearm was placed carefully along the edge of the plastic sheet so that the skin touched evenly along the whole length of the sheet, the sensation maximum was just above point *b*, and there was a definite

sensation of emptiness above point *a* corresponding to the black stripe in vision shown in Fig. 13-94 (dotted line). Unfortunately, the density of the nerve supply to the skin of the forearm is not large enough to make the contrast phenomena and the funneling strong enough for the 21-cm edge of the plastic sheet. In any case, the arm had to be placed carefully to have an even stimulus pattern.

When one edge of a vibrating frame was placed along the forearm, vibrations of 50 cps produced a sensation along the whole edge of the

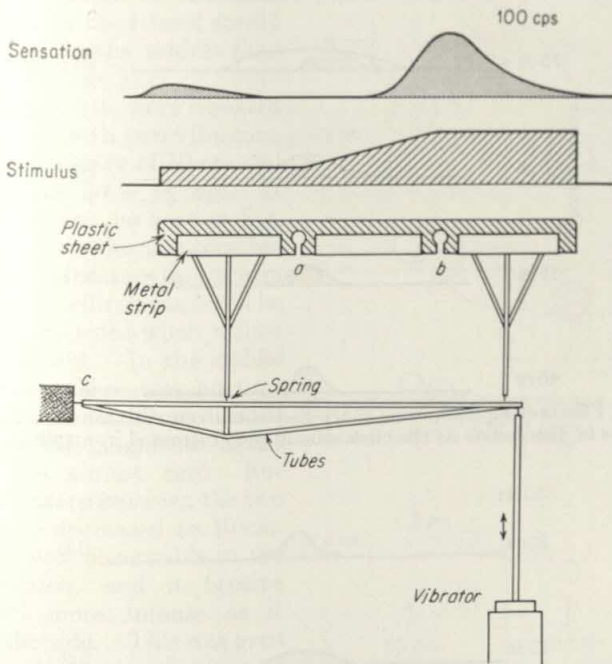


Fig. 13-95. Arrangement for the study of contrast on the skin. When the stimulus had the form of the crosshatched drawing the sensation was as indicated in the uppermost drawing.

frame. But if the frame was struck a sharp blow, produced by a condenser discharge through the electromagnetic driver, then the funneling action was strong, and only a few centimeters in the middle of the frame seemed to be vibrating. The strength of this funneling action could best be demonstrated by superimposing a series of sharp clicks of increasing amplitude onto the 50-cps vibrations of the frame, which were given a constant amplitude 20 db above threshold. As Fig. 13-96 shows, the wide spread of the 50-cps sensation is funneled more and more into the center of the click.

A continuous random vibration acts very differently from a series of sharp clicks. The random vibration produces a sensation that moves back and forth constantly along the edge of the vibrator at high speed.

This movement somehow disturbs the funneling action so that the superposition of the random vibration onto the smooth sensory pattern of a sinusoidal vibration spreads the pattern out laterally on both sides.

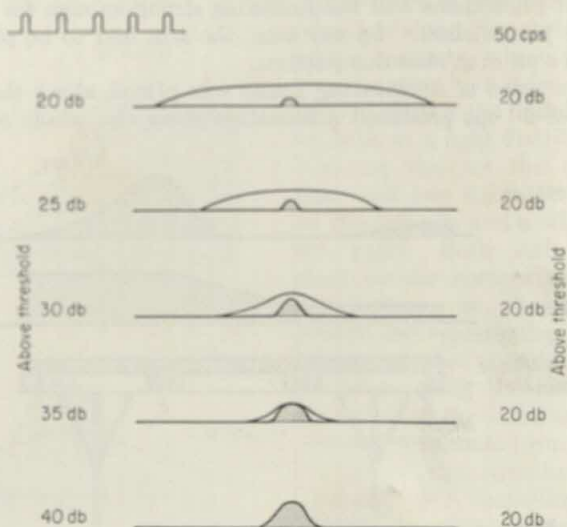


FIG. 13-96. Effects of superimposing sharp click stimuli on vibrations of 50 cps. Note the changes in distribution as the click stimuli were increased in amplitude.

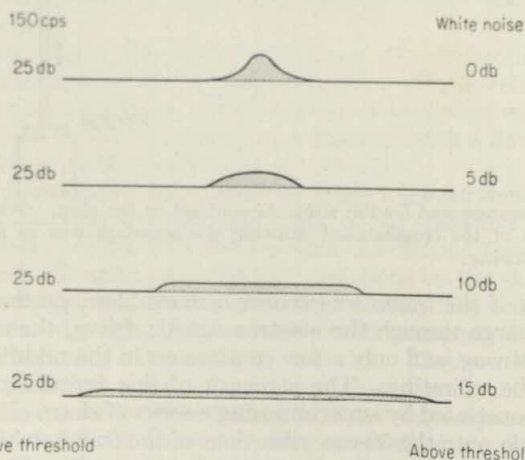


FIG. 13-97. Effects of superimposing white noise on vibrations of 150 cps.

At the same time the intensity of the sensation decreases, as shown in Fig. 13-97.

It is of interest to discover how the funneling works when there is a time delay such as is found in a rotating vibration or rotating sound.

It is known that even a small time delay is enough to funnel the whole sensation from one side to the other, but the changes in vibratory magnitude during the displacements of the sensation along the skin were very different from the findings in the ear. When a series of clicks is presented to one ear, and a similar series with a slightly different repetition rate is presented to the other ear, the click seems to travel from one ear to the other through the middle of the head, without changing its loudness or its apparent size. On the skin, however, the vibratory magnitude is smaller in the middle position than on either side, and at the same time the lateral spread is much larger in the middle than on either side (page 571).

These experiments were repeated on the forearm with two vibrators, one with a frequency of 50 cps and the other with $50 + \frac{1}{3}$ cps. It turned out, as can be seen in Fig. 13-98, that when the distance between the two vibrators on the arm was 20 cm, the vibrations could be felt only at the sides when a time delay was present. In the middle position, when there was no time delay, there was hardly any sensation, because the magnitude of the sensation was almost zero. But when the distance between the two vibrators was decreased to 10 cm, a sensation was observable in the middle position, and it became smaller and more intense as it moved to the side. This was even more noticeable for a distance of 5 cm. When the vibrators were 2.5 cm apart, however, the changes in vibratory magnitude during the displacements of the sensation were almost negligible, and at the same time the extent of lateral spread was almost constant, as the lowest drawing in Fig. 13-98 shows.

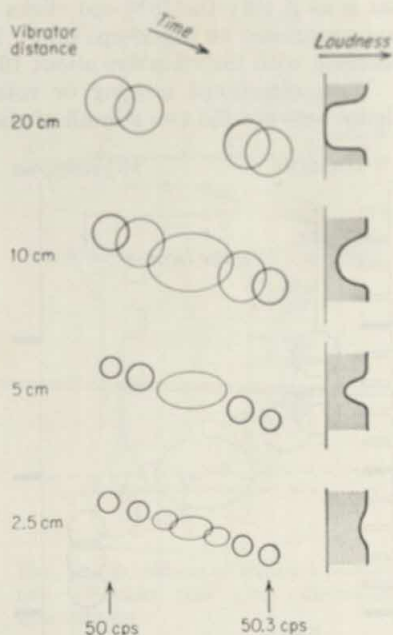


FIG. 13-98. Effects of a time delay between two vibrators applied to the forearm at different distances. The sizes of the circles or ovals represent the spread of the sensation and the diagrams on the right their magnitudes.

was almost constant, as the lowest drawing in Fig. 13-98 shows.

From this observation the conclusion can be drawn that if the distance between the two stimuli is greater than the action radius of the neural funneling, then when the rotating vibration is in the middle position the magnitude decreases considerably. But if the two stimuli are close together so that the neural interaction is strong, there is no magnitude change during the displacement from one side to the other. Since in the studies of the rotating tone no loudness changes were found as it moved from ear to ear, it seems likely that the neural interaction between

the two ears must be extremely great. This conclusion appears to be in agreement with the anatomical findings.

The funneling of the 50-cps vibration by a series of clicks in Fig. 13-96 shows that the funneling action, once produced, lasts a certain length of time, as it is able to suppress the 50-cps vibration between the separate clicks. But the active period of the funneling can be measured more precisely with the rotating skin vibrations. As can be seen from Fig. 13-99, if one vibrator produces a series of clicks at 50 pulses per sec, the displacements of the sensation from one side to the other are the same as if only the $10\frac{1}{3}$ -cps clicks were present, and 4 out of 5 pulses are suppressed on the 50-cps side. The measurements were made on the forearm with the vibrators about 10 cm apart.

With directional hearing or rotating sounds or vibrations, a time delay between the two stimuli of the order of 1.2 msec is enough to displace the sensation from the middle to one side. Evidently this type of funneling action acts with great rapidity. On the other hand, once a funnel is established, it generally takes longer than 30 msec to establish a new or perhaps a different funnel or to break up the old one. The time it takes to break up a once-established funnel plays an important role in room acoustics. It is well known that the echo produced by sounds reflected from walls is localized in the direction and pattern of the direct sound that strikes the listener first. This funneling action is the reason why we usually localize a speaker in the proper place, and not behind the walls, as we might locate him visually in a room lined with mirrors. The funneling of the room echo increases the loudness of the direct sound in a pleasant way. But the funneling action for the hearing of speech lasts only about 30 msec

(Haas). If the time difference between the echo and speech is too large, the echo is perceived separately and becomes disturbing.

On the skin of the left and right finger tips it is possible to obtain these "echoes" much the same as in hearing, except that the time relations are somewhat different. To study these phenomena, speech was recorded on a two-channel magnetic-tape recorder, and after the recording the two pickups were separated from each other to produce a time delay. One pickup was connected to the vibrator for the left hand and the other

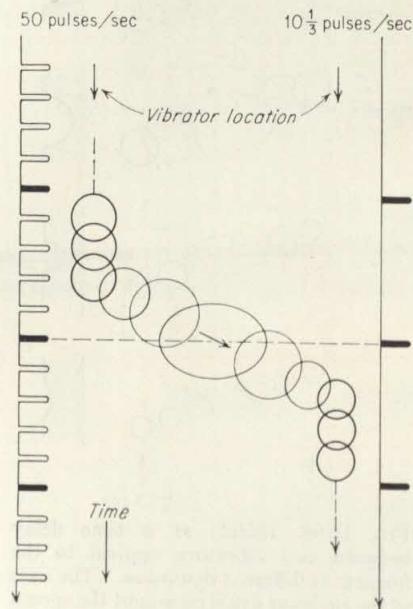


FIG. 13-99. The interaction of clicks at the rates of 50 and $10\frac{1}{3}$ pulses per second. The vibrators were on the forearm 10 cm apart.

to the vibrator for the right hand. For control observations the two pickups were attached to earphones, one at each ear. When the time delay between the two tracks on the tape was slowly increased from zero, the subject found first that a small time difference of about 1 msec shifted the whole sensation to one side. But it required a time difference of about 50 msec for the sensation on the one side to start to fall apart and the echo on the other side to become observable. For the hearing of speech the same subject found a time interval of about 25 msec enough to produce a distinct echo. The time interval for a distinct echo depends to some degree on the type of sound recorded on the tape. Certainly speech is more readily discriminated through an earphone than through the vibrator, and this seems to facilitate the separation of the echo from the original speech sound. This dependence of the fusion time of the echo on the discriminability of speech sounds seems to indicate that funneling may occur at different levels of the nervous system.

It is likely that contrast phenomena in vision and some analog on the skin are funneling actions produced by the lateral innervation at the level of the end organs. Directional hearing and the localization of rotating sounds and their analog on the skin occur at a higher level, for they are observed if the two stimuli are presented to the two different sides of the body. But there are some phenomena of funneling which must occur at a still higher level, for the times involved are of the order of 0.5 sec or more. Of this type of experiment only one will be described, which is an exact analog of an experiment done in hearing (page 375). The principle is shown in Fig. 13-100. Two vibrating frames were placed side by side on the surface of the forearm with a certain distance between them. By means of a switch the vibration could be alternately shifted from one vibrator to the other one without any interruption, every 0.5 sec. The vibrations were continuous random vibrations; the band width extended over the whole frequency range of the skin sensations.

When the distance between the two frames was small, a continuous sensation was produced as indicated in the upper drawing of Fig. 13-100.

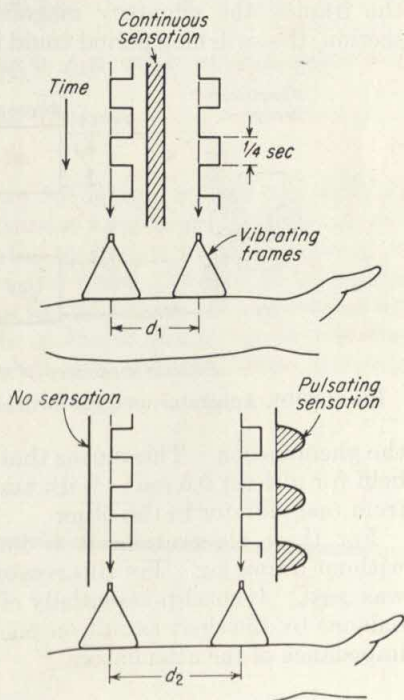


FIG. 13-100. Effects of distance between two vibrators that gave alternating stimulations.

But when a certain separation was reached between the two vibrators, the two frames could no longer be felt at the same time, but only one or the other, and when this happened a pulsating sensation was observed, as shown in the lower drawing. Depending on the distance between the frames, the vibratory magnitude, and the sensitivity of the skin section, the switching period could be increased to 1 sec without changing

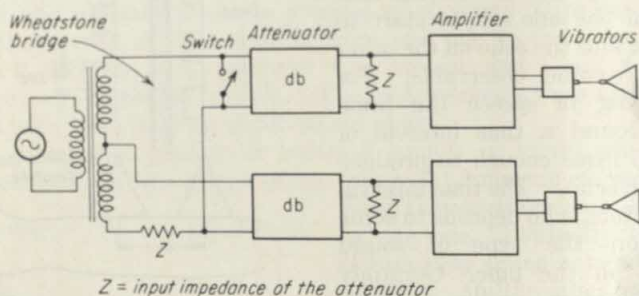


FIG. 13-101. Apparatus used for switching the stimuli between the two vibrators.

the phenomenon. This means that in this case a funnel, once established, held for at least 0.5 sec. With training the sensation could be switched from one vibrator to the other.

For these observations it is important that the switching be done without a time lag. For this reason, the equipment shown in Fig. 13-101 was used. It consists essentially of a Wheatstone bridge that is set out of balance by the short circuit on one arm of the bridge. Z represents the impedance of the attenuators.

CHAPTER 14

THE ELECTROPHYSIOLOGY OF THE COCHLEA

The electrical potentials that arise in living tissues raise two difficult questions. One of these is the particular anatomical location of the potential generators, and the other is the manner in which the energy is supplied. In general, the location of the place of origin of biological potentials is extremely difficult because the generators are surrounded by layers of insulating materials, and the voltages picked up outside the insulating layers are no more than scattered potentials often straying

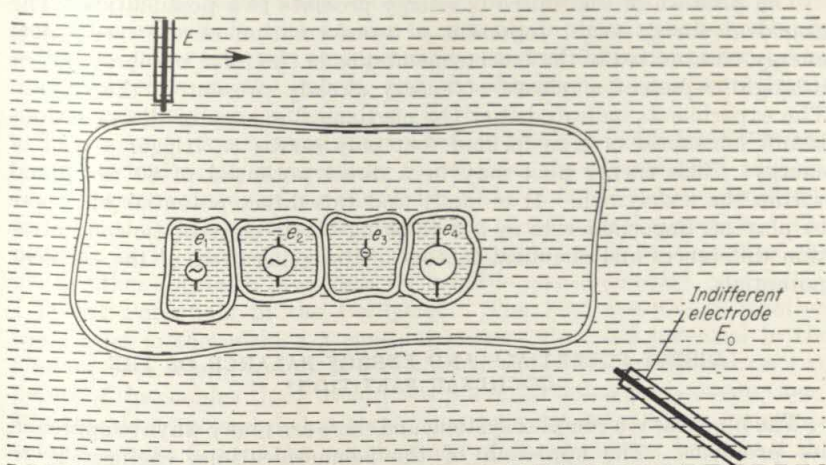


FIG. 14-1. The effects of insulating membranes on the electrical fields produced by potential generators.

far from their place of origin. The situation is illustrated in Fig. 14-1, where the generators e_1 , e_2 , e_3 , and e_4 are enclosed by two membranes. The problem is to locate these generators by applying two electrodes, an indifferent electrode E_0 remote from the region of interest and a small exploring electrode E placed at the point where we hope to find the generators. It is obvious that when the insulation of the membranes is high the stray currents outside have little to do with the location of the generators. This situation is further complicated by the fact that the membranes are thin and have large capacities, so that for alternating currents of high frequencies they lose their insulating properties and

become conductors. They then act as short-circuiting paths, and in the extreme case prevent any escape of currents to the outside.

The only solution of this problem is to insert the electrode as close to the generators as possible. For this purpose a vibrating electrode was developed that made it possible to pick up the potentials in the immediate vicinity of the vibrating tip, thereby localizing the mechanical vibrations at the site of the generator. With this technique it was shown that the potentials recorded from the round window of the cochlea represent an integration of the voltages arising in a large number of generators distributed along the basilar membrane. Such an integration of components of various amplitudes and phases does not allow us to draw conclusions about the voltages in the individual elements or to work out the pattern of vibration of the basilar membrane.

The vibrating electrode disclosed two features of the organ of Corti: (1) the microphonic voltage is proportional to the displacement of the basilar membrane and not to its velocity, and (2) shearing forces and displacements parallel to the surface of the basilar membrane play an important role in the production of the microphonics.

The problem of the source of energy presents two possibilities. The electrical energy might represent a transformation of the mechanical energy transmitted to the basilar membrane in the form of vibrations, or it might represent a release of energy already present in the tissues. The experiments indicated that the mechanical energy of the vibrations is not consumed or transformed, but only serves to trigger a pool of energy. This energy pool may be a direct potential of 80 mv found within the endolymph. It is likely that this direct potential will come to play an important role in our thinking about electrolytic concentration differences and chemical factors in the generation of the cochlear potentials.

DIRECT POTENTIALS AND ENERGY BALANCE OF THE COCHLEAR PARTITION*

The inner ear is a complex system, and there are many ways to approach its problems. The approach of the communications engineer is to consider the inner ear as a transducer, a type of dead tissue, that transforms mechanical movements into microphonics and nerve impulses. In this scheme a change in metabolism is usually described as fatigue or recovery. It cannot be denied that this type of simplification has been successful in describing many of the phenomena observed in the inner ear.

On the other hand, a more physiological approach indicates that a living organism does not represent a stable system but is something that is continuously building up in some parts and decaying in others. For instance, research with isotopes has made it clear that even so seemingly indifferent a substance as the fat in an organism is continuously exchanged.

* Article 58 as listed in the Author's Bibliography. Published in 1950.

In such a physiological system with a floating equilibrium a stimulus is not simply transformed; it upsets a whole series of equilibrium positions.

The main difference between the physical and the more physiological approaches becomes clear if we consider the energy principle. In a physical system the principle of energy constancy must hold, and if the ear is merely a physical system, there is a continuous flow of energy produced in the inner ear, and the frictional losses cannot be larger than the mechanical energy input. On the other hand, in a physiological system there is a continuous flow of energy, and by physiological processes the electrical energy of the ear can be supplied continuously from chemical energy. A stimulus modifies the equilibrium position of a physiological system, a function similar to that of the grid potential in a vacuum tube. Indeed, if the electrical energy produced in the inner ear is furnished by chemical energy, it can be larger than the mechanical energy of the stimulus.

In biology it is well known that most living tissues produce constant currents flowing from one part to another. Every growing root shows a potential difference between the tip and the developed parts. This phenomenon is particularly interesting in a frog's egg, which in the beginning is a sphere with no clue to indicate in which direction the egg will grow. The first sign to appear is a potential difference between two opposite points on the sphere, and the direction of these two points determines the position of the frog (Burr).

The present paper investigates whether there are phenomena in the inner ear that make it necessary to consider the physiological aspects. In the present status of our knowledge of the inner ear it is not profitable to argue the physical approach *versus* the physiological approach. The question is, in what part of the chain reaction called hearing does one or the other approach give hints for possible measurements?

Direct Potentials in the Perilymph. The first question is whether there exist in the cochlea a constant current flow and potential in the absence of a stimulus. It is true that if electrodes are placed on two points of the cochlea there usually is a potential difference between them. But this does not mean that there must be a constant energy consumption or current flow in the neighborhood of the electrodes, because if the salt concentration at the two points is not the same, there can be a potential difference between the electrodes without any current, just as is true of a liquid-junction cell. Fortunately the perilymph in the cochlea has the same properties along both scalae. It can be shown in the cochleae of man and the guinea pig, as well as in models of the inner ear, that vibrations of the stapes produce a streaming of the perilymph. For vibrations of lower frequency there is an exchange of fluid through the helicotrema between the two scalae, which seems to assure the homogeneity of the perilymph. Hence if there is a potential difference between two points of the perilymph, there must also be a current flow, with an energy consumption.

For the measurements, tiny holes were drilled in the bony wall of the cochlea of the guinea pig. Care was taken that the holes did not injure

any blood vessel on either the inner or the outer surface of the wall, so that no bleeding would occur. The tip of the electrode was placed in the middle of the scala, a position in which a displacement of the electrode did not affect the measured voltages. If the electrode touched the cochlear partition or the wall, the resulting displacement produced a change in the potential difference.

It was found best to drill a hole in the vestibule near one end of the longer axis of the footplate of the stapes, where the wall is very thin and contains no blood vessels. Therefore this point was used as the zero point for the potential measurements. In Fig. 14-2 the vertical arrows indicate the voltages relative to this reference point. The vestibular scala always showed a positive voltage, but in the tympanic scala the voltage near the round window was negative relative to the vestibule. The indifferent electrode placed near the wall of the bulla was usually 2 to 3 mv negative relative to the vestibule, but this value was variable.

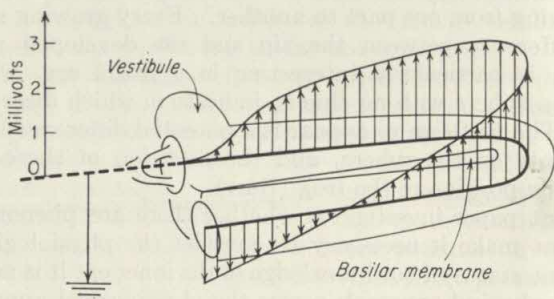


Fig. 14-2. Direct-current potentials in the perilymph of the vestibular and tympanic scalae.

If the cochlear partition was injured, particularly near the helicotrema, the positive potential often increased as much as tenfold. These injury potentials disappeared with time, but a new injury caused them to reappear.

In order to find out how much the holes in the wall of the cochlea influenced the measurements, the following experiment was carried out. If the voltages on the inner and outer sides of the round-window membrane are to be compared, the same fluid must be on both sides of the membrane in order that the electrode be always immersed in the same fluid. For this purpose a small drop of perilymph from the contralateral cochlea was placed on the outside of the round-window membrane. The voltage of this drop of perilymph relative to the indifferent electrode was about +2 mv, in accordance with Fig. 14-2. Then a hole was drilled in the wall as close to the round-window membrane as possible. There was no change in the potential of the outside surface of the round-window membrane relative to the indifferent electrode, which proved that a hole causes no disturbance as long as it does not injure the cochlear partition or the internal wall of the cochlea. The potential difference

between the inner and outer surfaces of the round-window membrane was of the order of 0.1 to 0.2 mv.

Figure 14-2 gives the impression that a positive potential is generated inside the cochlear partition. Because of the thinness of Reissner's membrane this positive potential is more effective in the vestibular scala than in the tympanic scala.

Effect of a Sound Stimulus upon the Direct Potentials of the Cochlea.

Now that it has been established that there is a continuous consumption of energy in the cochlea, it is of interest to discover whether this consumption is affected by an acoustic stimulus. For this purpose sound was conducted through a tube to the external auditory meatus of a guinea pig, and the microphonics and the changes in the d-c potentials between the round-window membrane and an indifferent electrode were observed simultaneously. Electric filters separated the a-c from the d-c potentials, and they were measured on two separate cathode-ray tubes. To make the d-c readings more sensitive, a part of the d-c voltage on the electrodes was compensated by a d-c voltage of opposite sign. In this way changes in the d-c voltage of the order of 10 μ v could easily be detected.

To make sure that there was no cross modulation in the electrodes or filters, a control experiment was carried out first. The two measuring electrodes were immersed in Ringer's solution. To the left and right of these electrodes were immersed two electrodes connected to an a-c source. Two additional electrodes outside of these last two were connected to a d-c battery. The internal impedances of the current sources were made very high. No cross modulation appeared when the sources were switched on and off. This held true even when the voltages picked up by the electrodes were about ten times as large as those picked up during the measurements on the cochlea.

The d-c voltage at the round window fell suddenly every time a sound of constant intensity was switched on, and consequently the positive potential of the round window relative to the indifferent electrode became smaller. Preliminary observations showed that at other points on the cochlea a constant sound stimulus often produced an increase of the d-c voltage rather than a decrease. The observations discussed in this section were always made at the round window, where the d-c voltage always decreased, relative to an indifferent electrode, when a sound of constant intensity was switched on. Therefore the term d-c fall will be used throughout the present section. The size of this d-c fall at the round window was proportional to the size of the microphonics produced at the same time. This relation is shown in Fig. 14-3. The proportionality does not hold for high sound pressures, where the amplitude of the microphonics is no longer proportional to the sound pressure. In general it was easier to measure the d-c fall inside the tympanic scala through a hole than on the outside of the round-window membrane, where the electrolytic conditions are not very stable.

To make sure that the d-c fall was not produced by a contraction of the middle-ear muscles, they were removed along with the eardrum and the

incus. Only the stapes was left. When the top of the stapes was brought into contact with the point of a needle and the needle was set into vibration, there was a d-c fall similar to that observed before.

It was found further that a displacement of the round-window membrane did not produce a sustained d-c fall if the voltages were measured inside the tympanic scala or if care was taken that, during the movements of the membrane, the position of the electrode relative to the

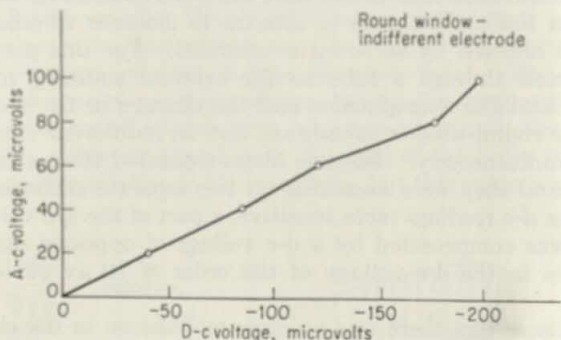


FIG. 14-3. Relation between direct and alternating potentials at the round window during stimulation with a tone of 800 cps.

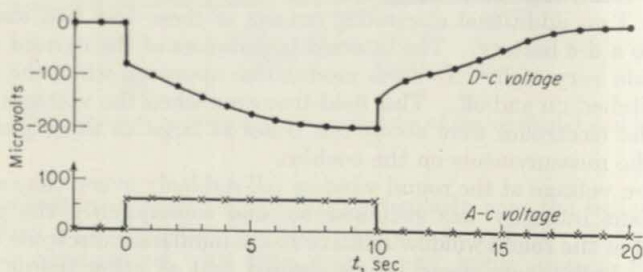


FIG. 14-4. Fatigue and recovery curves for the direct and alternating potentials at the round window during stimulation with 800 cps.

membrane did not change. This seems to indicate that the d-c fall is produced in the inner ear.

If the preparation was fresh, the introduction of a sound of constant intensity produced a d-c fall that was sustained as long as the sound was on and ceased immediately when the sound stopped. But if the cochlea was exposed to extremely loud sounds, or if the oxygen supply to the animal was reduced, the size of the d-c fall grew greater as the sound continued. This fact is shown for a specific case in Fig. 14-4. When the sound was turned off, the d-c voltage rose suddenly, but it took a long time for the original value of the potential to be fully restored. In contrast to this, the size of the microphonics shows no change at all for a constant intensity. There is a degree of independence between the

changes in the d-c potentials and the size of the microphonics produced by a sound.

The Three Different Potentials in the Cochlea. The potentials discovered by Wever and Bray (3) were differentiated into microphonics and nerve impulses by Saul and Davis and by Adrian (2). The question now is whether the d-c fall produced by a sound represents still another basic process. In an attempt to answer this question, the decay of the potentials accompanying the death of the animal were recorded. After the oxygen supply was stopped the microphonics produced by a constant sound decayed (a-c curve in Fig. 14-5). Similar observations were made by Wever, Bray, and Lawrence (2); Wever, Lawrence, Hemphill, and Straut. At the same time there was a d-c fall having a different slope. Usually the size of the d-c fall increased after the oxygen supply

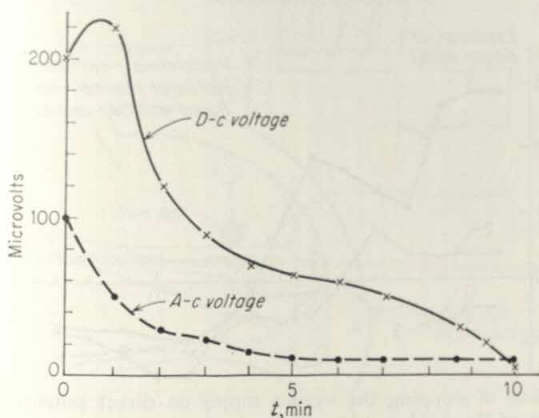


FIG. 14-5. Effects of oxygen lack on the direct and alternating potentials, for 800 cps.

was stopped, and it was not until later that it began to decrease. By changing the depth and duration of the narcosis the d-c fall could be modified (note the slope of the d-c curve of Fig. 14-5). The oxygen supply was curtailed by introducing a tube of considerable length into the trachea so that the animal partially rebreathed the exhaled air. If this condition was maintained over a period of about 15 min, at the end of which time the oxygen supply was completely cut off, the size of the d-c fall accompanying death sometimes remained constant for about 5 min before it began to decrease. But the amplitude of the microphonics, measured concurrently, decreased immediately after the oxygen supply stopped. Both the microphonics and the d-c fall were measured on the round-window membrane relative to an indifferent place near the outer surface of the bulla.

Usually, with increasing anoxia, first the neural potentials, then the microphonics, and finally the size of the d-c fall became smaller. Each of these three seems to go through a different process.

It was expected that when there was no stimulus the d-c potentials at various points in the perilymph would fall with the same slope; but,

as Fig. 14-6 shows, this did not occur. Therefore we must conclude that there are several different processes set up by anoxia.

Transformation of Mechanical Energy into the Electrical Energy of the Microphonics. The fact that with no stimulus there is a continuous d-c potential and a continuous consumption of electrical energy in the perilymph raises the question whether the energy of the microphonics is obtained from transformation of the mechanical energy of the cochlear partition or from the energy reservoir of the continuous d-c potentials. If it is a transformation of mechanical energy, then when the cochlear partition is set into vibration by a sudden push it will lose its mechanical energy both through friction and through the production of microphonics. Therefore the amplitudes of the cochlear partition and the microphonics will show a certain rate of decay. If the production of

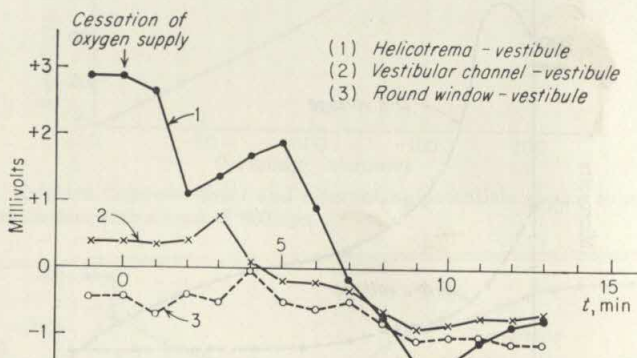


FIG. 14-6. Effects of stopping the oxygen supply on direct potentials recorded at different regions of the cochlea.

microphonics is now diminished, *e.g.*, by anoxia, the rate of the decay should change. If anoxia decreases the insulation of some membranes, the electromotive forces of the microphonics will be shunted through some new conductive pathways. Then, because of the smaller resistances, the consumption of the electrical energy may even increase. On the other hand, if there is a reduction of the electromotive forces of the microphonics, then the loss of electrical energy will be smaller, and the decay time will be prolonged.

To carry out this experiment a small iron ball was introduced through a hole in the top of the cochlea and was placed near the middle part of Reissner's membrane, as shown in Fig. 14-7. The cochlea was tilted so that this part of Reissner's membrane was in a horizontal position. The weight of the iron ball deformed the cochlear partition. When the ball was lifted suddenly by means of an electromagnet, the cochlear partition received a short, sharp pull. After several trials it was possible to adjust the position of the electromagnet in such a way that, when the current in the electromagnet was turned off, the iron ball fell back to its original position on Reissner's membrane. The microphonics were

picked up by one electrode placed near the iron ball and close to the modiolus and another electrode placed in the vestibule.

The iron balls were made from iron wire 0.05 mm in diameter. The wires were embedded in a plastic substance and then cut into cylinders 0.05 mm long. After the plastic was removed they were rotated between two glass plates with some emery powder. It was important that the balls be as round as possible, for otherwise the magnetic field rolled them on Reissner's membrane before they were lifted from it, and when this happened the pull on the cochlear partition was not sufficiently abrupt. It was difficult to place the iron balls at the proper place on the partition. A ball placed on the surface of the perilymph did not sink but floated away on the surface, driven by capillary forces.

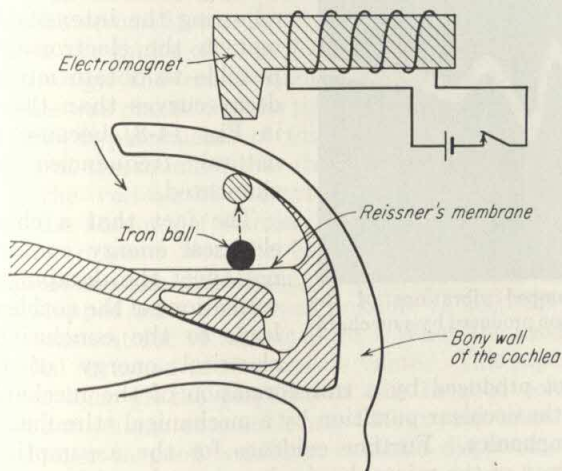


FIG. 14-7. Method of imparting a mechanical shock to the cochlear partition.

To avoid this difficulty, a small drop of perilymph was picked up on the tip of a platinum wire. With this wet wire the iron ball could be picked up from the glass plate. Then when it was placed on the surface of the perilymph it sank immediately, and could be positioned properly by means of the magnet.

The oscillations of the cochlear partition were measured when the ball was pulled away, because then there was no abnormal load on the partition. As a control, the ball was placed on the bony part of the cochlear partition and on the spiral ligament, and then the size of the microphonics was zero.

Figure 14-8 shows the first picture obtained, with the ball placed near the end of the cochlear partition. Here the natural period is 150 cps, and the amplitude ratio between two consecutive maximal excursions in the same direction is about 3:1. It should be pointed out that the vibratory mode of the cochlear partition for such a sharply localized displacement as produced by the iron ball is very different

from the mode produced by the movement of the stapedial footplate. This latter consists of traveling waves going toward the helicotrema.

After the iron ball had been lifted and dropped several times and the vibratory pattern had shown no changes with time, the oxygen supply

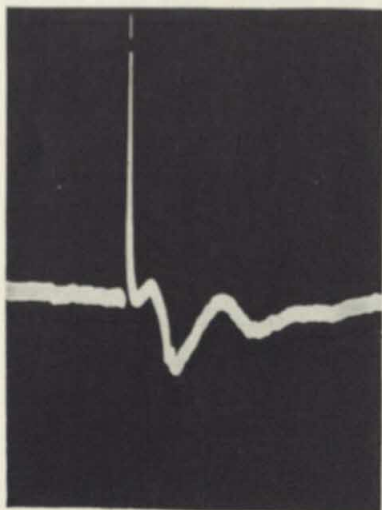


FIG. 14-8. Damped vibrations of the cochlear partition produced by a mechanical shock.

to the animal was reduced until the amplitude of the microphonics dropped to one-fourth of its normal value. When the amplification had been properly readjusted, no change in the decay curve could be detected. This experiment was repeated on many guinea pigs, always with the same results. By adjusting the intensity of the current in the electromagnet it was possible to obtain much smoother decay curves than the one shown in Fig. 14-8, because the higher natural frequencies were then eliminated.

The fact that a change in the electrical energy consumption did not affect the damping of the free oscillations of the cochlear partition leads to the conclusion that the electrical energy of the micro-

phonics is not produced by a transformation of the mechanical energy delivered to the cochlear partition by a mechanical stimulus.

D-C Microphonics. Further evidence for the assumption that the electrical energy of the microphonics is not produced by transformation of the mechanical energy can be obtained if it is possible to show that the amount of electrical energy caused by a given deformation of the cochlear partition is greater than the amount of mechanical work done. Such a measurement seems to be difficult when the cochlear partition is undergoing forced vibrations, because the energy loss resulting from friction inside the cochlear partition and in the surrounding fluid is not known. But it should be possible to measure the work done when a needle point is pressed against the cochlear partition, while at the same time the potentials produced by this deformation are measured across known resistances. If a single static deformation of the cochlear partition should produce a constant continuous potential—a d-c microphonic—this would prove that the electrical energy arising in the cochlea is from a nonmechanical pool of energy, perhaps an oxidation-reduction process.

The maximal value of the d-c microphonics that can be expected is of the order of 200 μ V. The whole measurement is reduced to the problem of finding an electrode that is suitable for d-c measurements. One was finally produced that could be duplicated within the limits of

20 μv , would maintain these limits for several hours, and at the same time was sufficiently small. Furthermore, the readings of this electrode were not affected by the protein content of the solutions, nor was there any measurable sign of polarization for the d-c potentials of 3 to 5 mv occurring in the perilymph.

In order to find out how long the d-c microphonics lasted after a single deformation of the basilar membrane, measurements were made first near the round window. A small hole was drilled in a corner of the round-window membrane, and through it one of the electrodes was inserted into the tympanic scala. The second electrode was inserted into the vestibule through a hole near the stapedial footplate. The d-c potential between the two electrodes was compensated by means of a battery and a potentiometer in such a way that the input to the d-c amplifier became zero. It was usually possible to hold this adjustment constant within the limits of 20 μv for a half hour. Then another hole was drilled through the round-window membrane, and through it a thin glass needle was placed with its tip just above the basilar membrane. Small and slow displacements of this needle did not change the d-c potentials; but at the moment that the surface of the basilar membrane was reached, the voltage of the tympanic scala became increasingly positive, and the amount of increase depended on how deep the tip of the needle was pressed into the basilar membrane with the micro-manipulator. When the displacement was stopped, the changes in the d-c potential stopped also, and it was possible to keep the value of the d-c potential constant for 10 min or more. When the needle was lifted, the d-c potential returned to its previous value. This experiment could be repeated as long as the preparation was in good condition. The maximal d-c microphonic obtainable was 300 μv ; but when the preparation was no longer in good condition, a static displacement no longer produced a d-c microphonic of constant size. Instead it fell slowly. Anoxia gave the same result.

If the displacement was too great, the d-c potentials suddenly jumped to a much larger value, which was either positive or negative. These were potentials of the injured cochlear partition, and when the needle was withdrawn, the potentials remained. With anoxia these injury potentials fell much more slowly than the microphonics.

The same experiment was repeated near the helicotrema. In that location it was much more difficult to keep the zero line constant. The removal of the eardrum, the malleus, the incus, and the tympanic muscles seemed to be necessary. The zero line could be considerably improved by adjusting the narcosis so that breathing was regular and approximately sinusoidal. Then a displacement of the zero line on the oscilloscope could be observed precisely. If the point of a needle was then pressed against the cochlear partition and a constant displacement of the partition was produced, a d-c microphonic of constant size again appeared between the perilymph near the helicotrema and an indifferent electrode. The size of the d-c microphonics remained constant for many minutes after an initial drop of a few per cent.

Energy Balance for a Static Deformation of the Cochlear Partition.

An examination of the internal structure of the cochlear partition leads to the expectation that for the production of a certain amount of electrical energy a displacement of Reissner's membrane would require less work than a displacement of the basilar membrane. This seems likely because the stiff parts of the basilar membrane must be moved before pressure can act on the internal parts of the cochlear partition where the microphonics presumably are produced. Therefore a point on Reissner's membrane near the helicotrema was selected for a measurement of the mechanical work done for a certain displacement of the point of a needle pressed against the membrane.

For the small displacements used the validity of Hooke's law can be assumed. If, for a downward movement, we let s represent the distance traversed from the point of first observation of a movement of the needle to the point where the movement is stopped, and if p represents the pressure exerted on the needle at the end point, then the work done is given by $A = \frac{1}{2} \cdot sp$. The greater part of this work is stored in the potential energy of the elastic membrane and can be recovered, as shown in Fig. 14-8, if the pressure is released and the membrane is allowed to swing back. Therefore only a small part of this mechanical work could be transformed into the electrical energy of the microphonics during the pressure on the membrane.

Here will be considered only one part of the electrical energy consumption, namely, the energy loss in the vestibular scala. This scala represents, from the electrical point of view, a pure fluid resistance of about 15,000 ohms. If a voltage difference exists between the helicotrema and the vestibule, a current must flow through this resistance, and the energy loss can be calculated. From Fig. 14-2 we can see that when there is no pressure on the membrane there is a constant potential difference between the helicotrema and the vestibule. Let us call this potential difference E_0 . The continuous energy loss is E_0^2/R . If the needle is pressed against Reissner's membrane, the potential of the perilymph near the helicotrema increases relative to the vestibule. Let us call this voltage increase E . Then the additional loss of electrical energy for a certain time interval t produced by the deformation of the membrane is given by

$$W = \frac{t}{R(2E_0E + E^2)} \quad (14-1)$$

The values in an actual case were $s = 10^{-3}$ cm, $p = 1.4$ dynes, $E_0 = 2$ mv, and $E = 0.3$ mv. For mechanical work, $A = 7 \times 10^{-11}$ watt-sec [10^7 dyne $\times$ cm = 1 watt-sec]. For electrical energy loss in the vestibular scala, $W = 8.6 \times 10^{-11}t$ watt-sec. These figures demonstrate that after a time interval of 1 sec the increase in electrical energy consumption produced by the pressure on the membrane becomes greater than the mechanical work done on the membrane.

From these experiments it is necessary to conclude that the electrical energy of the microphonics is not supplied solely by the mechanical

energy of the stimulus. Corresponding measurements made on the basilar membrane near the round window corroborated this conclusion. However, this conclusion holds only for microphonics produced by an animal in good condition, when a maximal voltage of 200 to 300 μv was obtained. If, for instance, in a dying animal the microphonics declined to a value around 10 μv this conclusion would no longer be valid for two reasons. First, the time t in Eq. (14-1) would have to increase to a very large value to fulfill the equation $W > A$, and the long times required could not be verified experimentally. Second, in a dying animal a static deformation of the cochlear partition no longer produces a continuous increase in potential. The potential increases immediately after the deformation and then falls slowly. It may be that these low-level microphonics are of entirely different origin, and it may be that they are produced by an energy transformation of the stimulus.

RESTING POTENTIALS WITHIN THE COCHLEAR PARTITION*

Evidence has already been given on the existence inside the cochlea of a lightly anesthetized guinea pig of continuous d-c potential differences between different places on the cochlea that appear not to be related to any acoustic stimulus. These resting potentials appear across the cochlear partition, *i.e.*, between the perilymph of the vestibular scala and the tympanic scala, and are of the order of a few millivolts. In the course of the measurement of these resting potentials it was observed several times that a minute perforation in Reissner's membrane immediately increased the potential difference between the two channels. Consequently, a special technique was developed to determine whether Reissner's membrane was still intact. The results suggest that there are structures within the cochlear partition that show potential differences larger than the differences found between the two cochlear scalae. The experiments to be described represent a preliminary attempt to measure these resting potentials inside the cochlear partition.

Force Required for the Perforation of a Thin Membrane. One of the first problems encountered was that of introducing microelectrodes into the cochlear partition with a minimum of damage to the surrounding tissues. Direct observation under a stereoscopic microscope made it evident that it is extremely difficult to perforate with a micropipette even so thin a membrane as Reissner's membrane without damaging the tissue around the opening. The pressure of the micropipette is distributed over a large area of the membrane, and a break may occur at some distance from the point of the micropipette.

Let us consider for a moment the maximum stresses S_{max} in a circular plate loaded at the center with a force P uniformly distributed over the area πr_0^2 . If t is the thickness and r the radius of the plate, then in an unsupported plate the relation between the maximum stress in the plate

* Article 64 as listed in the Author's Bibliography. Published in 1952.

and the force P is given by

$$P = \frac{\pi}{3} t^2 \frac{S_{\max}}{K} \frac{1}{1 - \frac{2}{3}(r_0/r)}$$

where K is a constant with an approximate value of 1. If the circular plate is fixed at the circumference, we have

$$P = \pi t^2 \frac{S_{\max}}{1.4 \log_e (r/r_0)}$$

as given by Hütte. These formulas are approximate. If we make the maximal stress $S_{\max}$ equal to the stress S at which the material breaks,

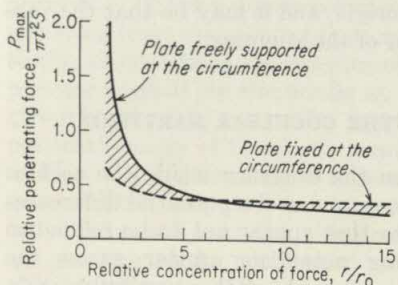


FIG. 14-9. Force required to penetrate a thin membrane in relation to the concentration of the force, expressed as r/r_0 where r is the radius of the membrane surface and r_0 is the radius of the penetrating point.

then $P_{\max}$ represents the force that penetrates the plate. In Fig. 14-9 the penetrating force is plotted for different radii r_0 of the pipettes. Biological plates such as Reissner's membrane are neither unsupported nor fixed at the circumference; consequently for them the perforating pressure falls in the hatched area of the figure. The perforating pressure decreases as the diameter of the pipette is reduced, until this diameter becomes one-third of the diameter of the plate. But a further reduction of the diameter of the pipette does not affect the perforation pressure. This may be the reason why a micropipette with a diameter of 5μ can be just as damaging to Reissner's membrane as a pipette with a diameter of 50μ .

This situation changes when we decrease the diameter of the micropipette to the point at which it is smaller than the diameter of a single cell. Now the force on the pipette acts only on the wall of the isolated plate formed by a group of cells. The formulas mentioned above show that the penetrating force P is proportional to the square of the thickness t of the plate. This tends to make the force P very small when the wall of a single cell is perforated. Thus we can expect a marked decrease in the penetrating force, not when Reissner's membrane is perforated as a whole at one time, but when the small pipette perforates the walls of the cells one after another and the perforating process of the whole membrane is spread out in time. This seems to suggest that the tip of the micropipette should be smaller than the diameter of the cell. Here again we have the same relations as those shown in Fig. 14-9, and a decrease in the diameter of the pipette to considerably below the diameter of a single cell would further decrease the perforating pressure. Micropipettes with a diameter of about $\frac{1}{3} \mu$ should therefore be used. Ling

and Gerard found also that the potentials of a single muscle fiber were more reproducible when electrodes with a diameter of less than $1\ \mu$ were used.

Measurement of the Potential Differences. When one micropipette is introduced into the perilymph of the vestibular scala and a second micropipette filled with the same electrolyte is introduced into the endolymph of the cochlear partition, the electrical potential difference between the two electrodes consists of the sum of three potential differences. First, there is a junction potential between the fluid of the electrode and the perilymph, produced by the different ionic concentrations in the two fluids. Then there is a potential difference across Reissner's membrane. It is this potential difference that is to be measured. Finally, there is the potential difference between the endolymph and the fluid of the second electrode—again a junction potential. The junction potentials are of the order of a few millivolts. When the electrodes are immersed in the same fluids they cancel each other, but

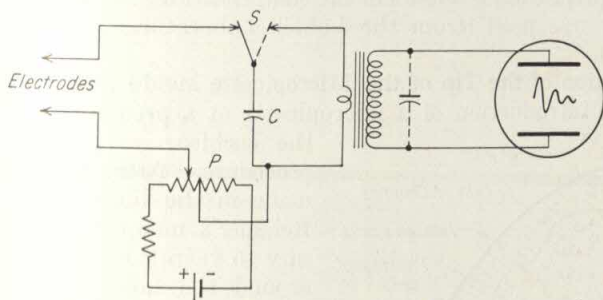


FIG. 14-10. An amplifier for d-c pulses, with high input impedance.

in the present experiment this did not occur. A calculation of the size of the junction potentials is not possible at the moment because we know relatively little about the chemical properties of perilymph and endolymph.

As far as the writer knows, Tower was the first to show that junction potentials can be eliminated under certain circumstances. It was Planck who calculated the junction potential between two different solutions, and he found that with binary salt solutions the magnitude of the potential is proportional to the difference in mobility of anions and cations (see also Nernst). Thus if the mobility of anions and cations is the same, there is no junction potential. Potassium chloride fulfills these requirements to some degree. If other ions are present in addition to potassium chloride, the junction potential can still be broken down, as is known, by using a high potassium chloride concentration. In the present experiment the micropipettes were filled with 3 *M* potassium chloride solution, and silver chloride electrodes were used.

Thin micropipettes have a high resistance, and a static electrometer is probably best for measuring the potential differences. Here a pulse amplifier was used. A schematic wiring diagram is shown in Fig. 14-10.

The potential differences on the electrodes charged a small condenser *C*, and this condenser was then discharged once every second through a transformer. The sharp discharge current produced a damped oscillation in the circuit formed by the transformer coil and its own winding capacity. These oscillations were amplified and observed on an oscilloscope. The potential difference on the electrodes was compensated by means of a calibrated potentiometer *P* until oscillations were no longer seen on the oscilloscope. If the capacity *C* was kept small, the number of coulombs going through the electrodes could be kept small also. The only difficulty was to keep switch *S* in good working condition. Appropriate shielding of the equipment prevented condenser *C* from picking up voltage from a free end of wire during the movement of the switch. To compensate the potential differences it was appropriate to amplify the electrical oscillations and to insert between the amplifier and the oscilloscope a self-actuating logarithmic attenuator. This attenuator emphasized the small voltages and decreased the large voltages, and it permitted rapid and precise adjustments of the compensation. A Kay-Lab Logaten attenuator was used (from the Labell Laboratories, Inc., San Diego, California).

Localization of the Tip of the Micropipette inside the Cochlear Partition. The introduction of a micropipette at a predetermined point on

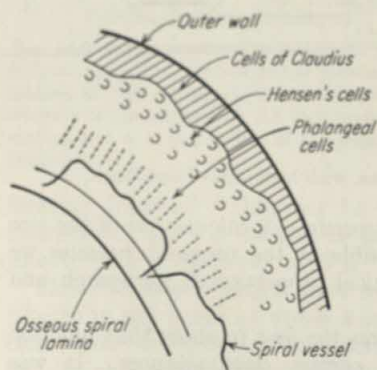


FIG. 14-11. Schematic view of the cochlear partition of a guinea pig, seen through Reissner's membrane.

the cochlear partition is a subtle procedure. After a small hole was made in the bony wall just above Reissner's membrane, it was necessary to keep the surface of the bone around the hole wet, so that the perilymph coming from inside did not form a drop but spread along the surface of the bone and produced a flat boundary between perilymph and air. If a spherical boundary was produced, the cochlear partition as seen through the microscope was considerably distorted.

For this same reason the diameter of the immersed part of the micropipette had to be as thin as possible, for the distortion of the boundary between the perilymph and air decreased rapidly with the size of the pipette because of capillary forces. Through the hole of a freshly opened cochlea a picture like that shown in Fig. 14-11 could usually be seen. Most fascinating was what looked like a number of round oil droplets lying on a flat membrane. The flat membrane consisted of the cells of Claudius, and the oil droplets were the large cells of Hensen. The ridge formed by the cells of Hensen had a distinct outer border with a characteristic shape. Closer to the modiolus, radial stripes could be seen, and they were the hair cells and phalangeal cells. Deep below the level of the cells of Claudius was the

spiral vessel in which red blood cells were seen moving at high speed. There were many recognizable landmarks. In a dying cochlea, the cells of Hensen became opaque, and in general the structures were more readily discernible. With experience it was possible to judge the decrease of the microphonics from the opalescence of the cells. To increase the visibility of the opalescence, violet light was used to illuminate the bony wall of the cochlea from one side. But in general, the better the condition of the cochlea, the less that was seen.

Landmarks in the vertical dimension were harder to find. The vertical slide on which the microelectrode was fixed was calibrated in microns, and by the use of microscopic slides of the cochlea it was possible to evaluate the expected distances. Most often the surface of Reissner's membrane was used as a reference point. When the electrode was pushed down it was easy to detect the moment at which its point touched Reissner's membrane. It was only necessary from time to time to give the electrode a small lateral displacement during its downward movement. As long as the tip of the electrode was free, it followed these movements closely, as could be seen in the microscope. But if the electrode was rather thin and elastic, the moment its tip touched Reissner's membrane it became immobilized, and a sudden jump in the potential difference occurred.

The depth at which the electrode reached the cells of Claudius could be recognized by observing the sharp border of the cells of Hensen. As shown in Fig. 14-12, a pressure on the cells of Claudius displaced the cells of Hensen toward the outer wall of the cochlea. This point too was characterized by a sharp jump in the potential difference between the perilymph and the electrode in the cochlear partition.

Potential Differences inside the Cochlear Partition. From the anatomical standpoint the most convenient location for measurement of the potentials inside the cochlear partition seems to be a point on the partition about 15 mm away from the footplate of the stapes. The cochlear partition around the helicotrema is not suitable because the partition there is flat, Reissner's membrane comes close to the organ of Corti, and the different cells cannot easily be discriminated. Closer to the footplate of the stapes the cochlear partition is too thick, and it is difficult to push an electrode from one scala to the other.

A representative set of measurements for the location at 15 mm is shown in Fig. 14-13. The dotted lines *a* and *b* represent the paths along which the microelectrode was pushed down. On left and right sides

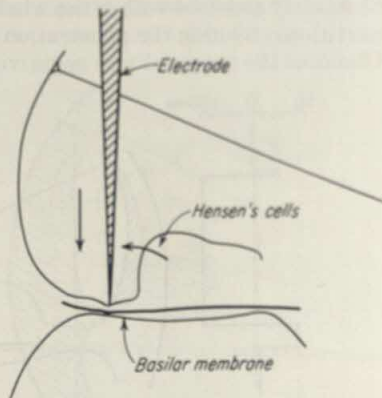


FIG. 14-12. The movement of the cells of Hensen is a sign of contact between the electrode and the cells of Claudius.

of the figure are the corresponding voltage differences between an electrode placed in the perilymph of the vestibular scala above Reissner's membrane and an electrode immersed to various depths in the cochlear partition.

During the time of perforation of Reissner's membrane, the perforating electrode was negative relative to the vestibular scala. This potential measured about -20 mv and may have been even higher, because the equipment was not suitable for precise measurements on single cells. After the perforation of Reissner's membrane the potential jumped suddenly to a positive value of about $+50$ mv and remained absolutely constant within the whole endolymphatic space in the cochlear partition. During the penetration of the cells of Hensen and the cells of Claudius the potential was negative and of the order of -40 mv. Inside

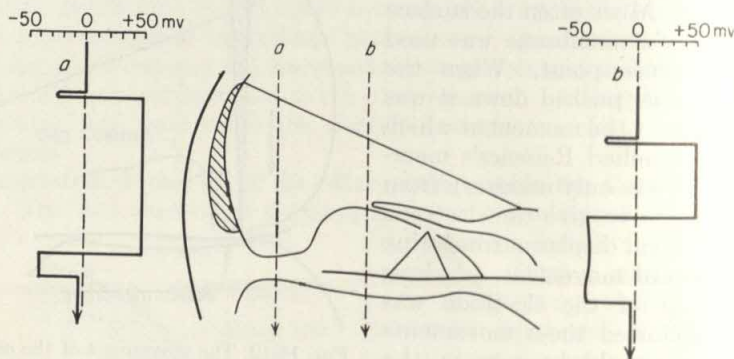


FIG. 14-13. Changes in the d-c potential during a downward movement of the electrode at two positions as shown.

these cells there was always a small fluctuation of the potentials. After the basilar membrane had been perforated, the negative potential fell back to a value of about -2 mv and remained there during the further downward movement of the electrode.

In some trials the retraction of the electrode gave exactly the same position-voltage pattern as during the downward movement of the electrode, except that the jumps in voltage on the border of the surfaces were less sharp. Sometimes, however, the voltage at a given place on the cochlear partition decreased with time and could not be brought back if the electrode was inserted into the cochlear partition a second time. The reason for these peculiar differences is that under certain circumstances even a very thin and elastic micropipette can produce great damage during penetration. This situation is illustrated in Fig. 14-14. On the left side of the drawing, the direction of the downward movement of the pipette is exactly parallel to the axis of the pipette. The damage produced in the tissue below the covering membrane, represented by a heavy horizontal line, does not exceed the diameter of the pipette. On the other hand, the drawing on the right represents a situation in which the direction of movement of the pipette is not parallel to the axis of the pipette. After the surface of the tissue

had been penetrated, there was a parallel displacement of the pipette, and the pipette began to bend. Then the tip of the pipette often produced large cuts in the radial direction. The relative stiffness of surface and deep layers of the tissue determined the amount of damage. As preliminary experiments showed, in brain tissue and in the auditory nerve this type of damage under certain conditions can produce a considerable amount of injury. Therefore great care was taken to adjust the axis of the pipette exactly parallel to the axis of the slide. In order to check this orientation, the cross hairs of a microscope were adjusted to the point of the pipette, and the direction of the slide was changed until an up-and-down movement of the pipette showed no displacement of the axis of the pipette relative to the cross hairs. This happens only

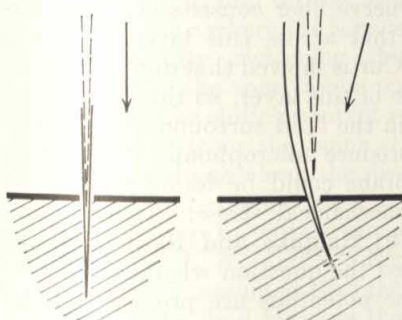


FIG. 14-14. On the left, the movement is along the axis of the electrode. On the right, it has deviated from this axis, bending the electrode and producing radial cutting of the tissue.

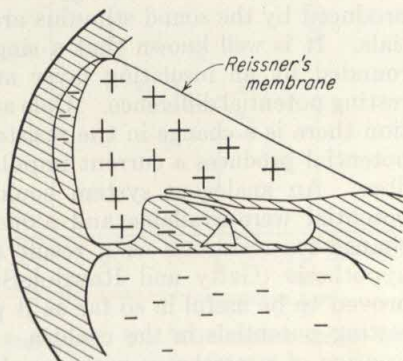


FIG. 14-15. The voltage pattern inside the cochlear partition relative to the perilymph above Reissner's membrane.

when the pipette is exactly straight. The pipettes have to be pulled mechanically.

The experiments showed that the more carefully the perforation of the cochlear partition was made, the higher were the potential differences obtained. The potential difference between the perilymph and the endolymph at the location of 15 mm was reproducible within 10 per cent, and the potentials inside the cells within 20 per cent. In spite of this the potentials shown in Fig. 14-13 are not to be considered as definite until the role of anesthesia, oxygen supply, etc., have been investigated.

Near the round window it was also easy to measure the potential difference of the endolymph relative to the perilymph of the tympanic scala. The endolymph had a potential of +80 mv, and the reproducibility was 5 per cent. The cells had a potential relative to the perilymph of -40 mv. The vascular stria inside the cochlear partition was always negative, but the spiral ligament did not show a potential difference relative to the perilymph. A sketch of the pattern of the potential inside the cochlear partition is given in Fig. 14-15, with the size of the

signs representing roughly the magnitude of the potential difference relative to the perilymph of the vestibular scala.

Inside the organ of Corti there are at least three tunnels running along the cochlear partition. At the present time, instruments are not fine enough to measure the potentials inside these tunnels or inside the tectorial membrane.

All the potential differences described dropped slowly during oxygen deprivation and after death.

The potential difference between the endolymph and the organ of Corti is surprisingly high, especially near the round window. It will be interesting to discover to what extent the different potentials produced in the cochlea by a sound stimulus are basically independent phenomena produced by sources of energy in the cochlea, or whether the potentials produced by the sound stimulus are a consequence of the resting potentials. It is well known that a single nerve fiber consists of a core surrounded by an insulating layer and that across this layer there is a resting potential difference. Cole and Curtis showed that during stimulation there is a change in the resistance of this layer, so that the resting potential produces a current impulse in the fluid surrounding the nerve fiber. An analogous system could produce microphonics if a resting potential were available and a membrane could be found that would change its resistance as a result of mechanical stress. This working hypothesis (Gatty and Rawdon-Smith; Hallpike and Rawdon-Smith) proved to be useful in so far as it posed the question whether there are resting potentials in the cochlea. The potentials are present, but the location of a membrane with variable insulation is still a problem.

PATTERN OF ELECTRICAL RESISTANCE IN THE COCHLEA*

For a thorough understanding of the cochlear microphonics it is necessary to investigate the electrical geometry of the cochlea, because only with a knowledge of the voltage and resistance patterns is it possible to form an over-all picture of the electrical situation in the cochlea. In the following measurements the whole cochlear partition is considered as a single layer. In earlier mechanical studies the partition was similarly considered as one membrane, and this made it possible to obtain a first approximation to the pattern of vibration. No doubt the voltage, resistance, and capacitance patterns of the whole cochlea will eventually be determined. When this is done we shall have, in addition to the well-known histological anatomy of the cochlea, a kind of anatomy that may be called the electroanatomy of the cochlea. The resistance pattern of the cochlea is important in calculating the energy dissipation attendant upon the microphonics. This dissipation of electrical energy must be considered side by side with the dissipation of mechanical energy. Stevens and Davis have already made an estimate of the electrical resistance between the two scalae of the cochlea near the round window.

* Article 61 as listed in the Author's Bibliography. Published in 1951.

Techniques for Measuring Resistance. When the resistance of a tissue is measured in a Wheatstone bridge, the resistance of the electrodes is added to the tissue resistance. The resistance of the electrodes consists of a transmission resistance between the surface of the metal and the fluid plus a resistance produced by the concentration of the electrical flow lines in the neighborhood of the electrodes. The over-all resistance of the electrode can be measured with the same techniques that are used for measuring the grounding resistance of a lightning rod. According to

the method of Wiechert, the grounding resistance of a lightning rod, R_x and R_y , can be measured by introducing an auxiliary electrode E (see Fig. 14-16). By switching the earphone P to the auxiliary electrode E it is possible to find on the wire (AB) a distance c where the tone is a minimum. By switching the earphone to Y , the tone minimum appears when the sliding contact is at a distance a from the point B .

The drop in voltage along the distances c , b , and a must then be equal to the drop in voltage along the resistances R_x , R_y , and R . For the cochlea it is assumed that the resistance of the fluid between the two electrodes X and Y is so small compared to the resistance of the electrodes that the position of the auxiliary electrode E has no effect upon the adjustments of the sliding contact. For the resistances of the electrodes we have then $R_x = Rc/a$ and $R_y = Rb/a$.

A comparison of the different types of nonpolarizable electrodes showed that a platinum electrode plated with platinum black gave good results.* For measurements in the cochlea the maximum diameter of the electrode wire could not exceed 0.1 mm. A platinum electrode of the type described gave an over-all resistance of about 1000 ohms when immersed in the perilymph of the cochlea. This large resistance decreased the precision of the measurements, because the resistance to be measured was of about the same value.

It is possible to eliminate the effects of electrode resistances by using the electrodes only for voltage measurements, for then no current flows through them. Therefore, as far as possible, the resistances in the cochlea were determined by inserting two voltage electrodes at the points between which the resistance was to be measured, while at the same time a known current was led through the field of measurement (see

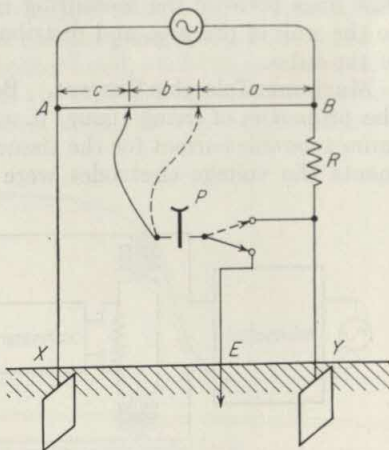


FIG. 14-16. The Wiechert a-c bridge for measuring ground resistance.

* The platinum electrode was made a cathode in a plating solution consisting of 1 part platinum chloride, 0.008 part lead acetate, and 30 parts water, by weight. The current density was 0.03 amp per sq cm.

Fig. 14-17). The resistance was calculated according to Ohm's law. The current I through the tissue was measured with a voltmeter inserted symmetrically relative to ground. The amplifier was a differential type with an attenuation of 80 db for voltages to ground.

Measurements of the resistance of the fluid column in a tube have shown that the distance between the current-carrying electrode E_1 and the voltage-measuring electrode E_3 (as well as that between E_2 and E_4) should be at least as great as the diameter of the tube, in order that the flow lines between the measuring electrodes E_2 and E_4 may be parallel to the wall of the tube and distributed evenly through the cross section of the tube.

Maximum Tolerable Current. Because an electric current may change the properties of living tissue, it was necessary to determine the maximum tolerable current for the tissue of the cochlea. For these measurements the voltage electrodes were connected to a harmonic analyzer.

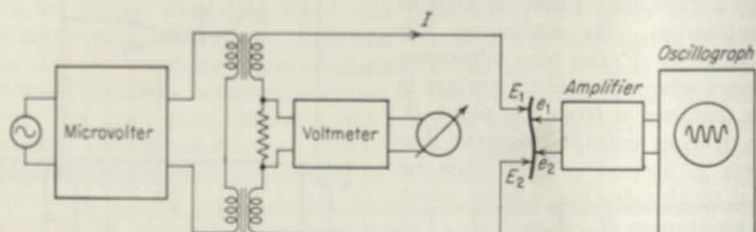


FIG. 14-17. Circuit for measuring tissue resistance in terms of voltage drop.

A current of 1000 cps was introduced into the measuring path by a second pair of electrodes and was adjusted so that the differential voltage from E_3 to E_4 was about $10 \mu\text{v}$. A third pair of electrodes introduced the current for the breakdown tests. The frequency of this current differed a little from 1000 cps, and could therefore be distinguished from the measured voltages. With all bad contacts and all rectifier types of current-measuring equipment eliminated, it was first found for a wire-wound resistance that a breakdown current did not affect a 1000-cps voltage across the path being considered. Then the same independence was established for a physiological solution into which all six electrodes were immersed.

After these preliminary experiments had been carried out, three holes were drilled close to the round window in the tympanic scala of the cochlea of a guinea pig. Three indifferent electrodes were placed on the neighboring muscles so that the currents were made to flow from the tympanic scala to the indifferent electrodes. The observations then showed that a current flow of 1 ma from the round window to the body did not influence the resistance across the cochlear partition. The resistance between the round window and the body is about 2000 ohms. As the measured voltage across this resistance was $10 \mu\text{v}$, the measuring current had a value of 5×10^{-6} ma. We are assured therefore that the measuring currents used in these experiments were within physiological

tolerances. The microphonic voltage between the round window and the body can be about 100 μ v, and currents of the order of 5×10^{-4} ma can occur in normal stimulation of the ear.

In the second experiment the microphonics were used to determine the maximum current tolerable without changing the normal function of the cochlea. The 1000-cps electric generator was turned off, and an air-borne tone of 1000 cps was led to the ear of the guinea pig. Microphonics of 1000 cps were observed with the harmonic analyzer, and the sound pressures were adjusted so as to be just detectable. These microphonics were maintained as long as the current going through the cochlear partition was less than 3 ma. On the other hand, when the sound pressure was increased to a value beyond which the microphonics did not increase further with increasing sound pressure, then, as Fig. 14-18 shows, a

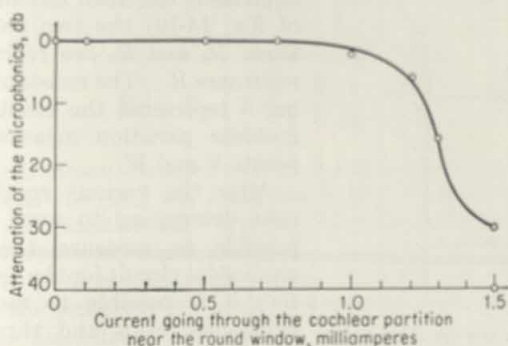


FIG. 14-18. Effect on the cochlear microphonics of passing direct currents through the cochlear partition in the region of the round window for a period of 10 sec.

current of 1 ma through the cochlear partition near the round window decreased the microphonics by 2 or 3 db. A still larger current produced a greater decrease, indicating that there was a breakdown in the tissue. Some recovery was observed, but it was usually of the order of only 6 db. During the measurements it was important to make sure that there was no fluid between the round window and the middle ear, because this fluid short-circuits the current through the cochlea.

Input Impedance of the Cochlea near the Round Window. The labyrinth consists of a great number of membranes and fluid-filled cavities, which complicates the picture of the current distribution. In order to make a reasonable guess about the currents in the different parts of the cochlea it therefore is necessary to think of many flow lines squeezed together here and there to form a network. The more resistances we use in the construction of the network, the closer it approximates the real situation.

In drawing *a* in Fig. 14-19, which is a schematic representation of the labyrinth, we see that the vestibular organ as a whole has a certain resistance toward the body. The vestibular system leads to the vestibule, where all the flow lines of current through the vestibular organ are

squeezed together. The path of these flow lines can be represented by the resistance R_3 , which for a grounded animal represents the grounding

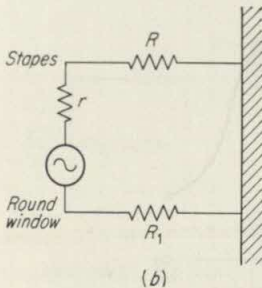
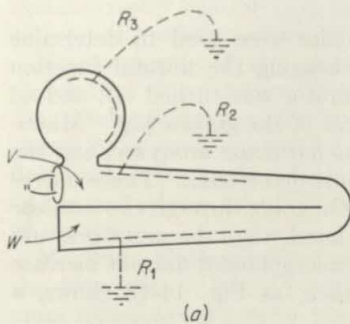


FIG. 14-19. Schematic drawing of the inner ear, showing the resistances between it and the body of the animal. Resistance r is that between points V and W.

near the round window, and electrodes were inserted into them. These two electrodes were connected to the ends of a potentiometer.

resistance of the whole vestibular system measured from the footplate of the stapes (point V) to the body. Each of the two cochlear scalae has a grounding resistance also. In the guinea pig, the top part of the cochlea stands free in the air of the bulla, and we are probably safe in assuming that the grounding resistances R_1 and R_2 are attached closely to the round window and the stapes, respectively. In the equivalent electrical circuit (drawing b of Fig. 14-19) the two parallel resistances R_2 and R_3 are replaced by the resistance R . The resistance r in drawing b represents the resistance of the cochlear partition measured between points V and W.

After the various resistances have been determined to some degree it is possible to measure them. In the equivalent circuit for the vestibular system it is possible to measure three resistance ratios and three combined resistances. In order to measure the resistance ratio R/R_1 , two holes were drilled in the cochlea, one near the footplate of the stapes and the other

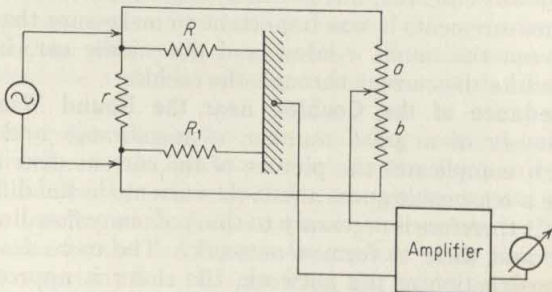


FIG. 14-20. Circuit for measuring the resistance ratio R/R_1 .

The sliding contact on the potentiometer was connected to one pole of the differential amplifier, as shown in Fig. 14-20. The other pole of the amplifier was connected to the indifferent electrode on the

animal. By using two other electrodes to introduce a voltage between the stapes and the round window, it was possible to find, with a sliding contact, a point on the potentiometer where no voltage was produced relative to the indifferent electrode. The ratio between the two arms of the potentiometer gave the ratio R/R_1 . It was also possible to determine the ratios R/r and R_1/r .

If R_0 is the measured resistance between the stapes and the indifferent electrode, r_0 the measured resistance between the stapes and the round window, and R_{10} the measured resistance between the round window and the indifferent electrode, then the resistances that constitute the electrical counterpart are

$$\begin{aligned} R &= R_0 \left(1 + \frac{R/r}{1 + R_1/r} \right) \\ r &= r_0 \left(1 + \frac{1}{R/r + R_1/r} \right) \\ R_1 &= R_{10} \left(1 + \frac{R_1/r}{1 + R/r} \right) \end{aligned}$$

So that these measurements could be made quickly and easily, three measuring electrodes and the three electrodes conducting the current were led to a combined switch. For the three unknown resistances there were six measurements, which provided a check on the precision of the measurements. The electrodes were made of Taylor wire with a diameter of 0.01 mm; the length of the free (uninsulated) end of the wire was 0.2 mm. The diameter of the holes in the bony walls of the cochlea was adjusted so that the electrodes fitted snugly. Sometimes the eardrum was removed. This made it possible to see any accumulation of fluid between the stapes and the round window. The footplate has an elliptical shape, and near one of its sharp ends the wall of the vestibule around the footplate is thin and contains no blood vessels. It was easy to drill a hole in the vestibule there and to insert the electrodes. It was more difficult to drill a hole in the tympanic scala near the round window. It was always necessary to use special illumination and a magnification of at least seventy times to find a place in the bony wall free of blood vessels.

The distance between the electrodes carrying the current and the voltage electrodes was about 0.2 mm. To be sure that the distribution of the flow lines did not affect the measurements too greatly, the current-carrying electrodes were sometimes interchanged with the voltage-measuring electrodes. This procedure made a change of about 5 per cent in the measured resistance.

For the cochlea of the lightly anesthetized guinea pig the following values were obtained, representing the means of measurements on six animals, *i.e.*, twelve ears: $r = 2250$ ohms, $R = 3700$ ohms, and $R_1 = 8500$ ohms.

The value of r was highly stable and showed a range of only about ± 10 per cent for the different animals. R and R_1 varied about twice

as much. It was obvious that when the operation was not meticulously clean the value of the resistance went down. If the current-carrying electrodes were too close to the voltage electrodes, the measured resistance went up. The impedances measured with 1000 cps did not show a capacitative component. This means that the impedances were determined primarily by the resistances of the fluid column and the resistances of the supporting cells. The active separating membranes did not play a role, and even the death of the animal did not seriously alter the value of the measured resistances. To determine the influence of the size of the cochlea on the value of the resistances, the same measurements were made on the ear of a sheep with the following results: $r = 1800$ ohms, $R = 2200$ ohms, and $R_1 = 3600$ ohms. These measurements were made half an hour after the sheep was killed. Because no essential changes occurred during the death of the guinea pig, it is probable that these values are not far from those in a living animal.

To measure R_3 alone, the cochlea of the guinea pig was extirpated. It was found that R_3 was at least three or four times larger than R_2 . These measurements were not very precise because it was difficult to keep the injured parts of the cochlea dry and to prevent bleeding.

It is of special interest to know the anatomical location of the grounding resistance between the cochlear scalae and the body. When the voltage difference in the microphonics between the round window and an indifferent electrode was measured it was found that these voltages decreased rapidly as the electrode was moved away from the round window along the surface of the free-standing cochlea. This fact seems to indicate that the bony wall of the cochlea is a good insulator. As a further test, resistances R , r , and R_1 were first measured in the normal guinea pig. Then all the free part of the cochlea was surrounded by cotton saturated with physiological solution, but care was taken to keep the surface near the round window dry. The wet cotton pack was directly connected with the indifferent electrode. This treatment produced no change in the values of resistances R , r , and R_1 . Therefore, as the grounding resistances are not located in the bony wall, they must lie in the internal part of the cochlea.

It can be assumed that resistances R_1 and R_2 depend upon the nerve tracts and blood vessels going into the modiolus. Accordingly, resistance R_3 is determined by the resistance of the nerve tracts and blood vessels going from the vestibular system to the brain. This assumption was proved by sucking away part of the brain close to the internal auditory meatus while keeping the surfaces dry, whereupon resistances R_1 and R showed a definite increase. Furthermore, the whole bulla of the guinea pig was removed from the skull, and the surface was cleaned. Then when two indifferent electrodes, one for the current conduction and the other for the voltage measurement, were introduced into the acoustic nerve the three resistances R , r , and R_1 remained the same as for the cochlea *in situ*. Therefore the main grounding pathway of the cochlea is through the acoustic nerve to the brain.

The grounding through the acoustic nerve represents a continuous

grounding all along the cochlear partition because of the blood vessels and nerves entering the partition from within the modiolus. Consequently there must exist considerable cross conduction between the different turns of the cochlea. In order to estimate the size of the grounding resistances within the cochlea, all the fluid of the cochlea was sucked away, the tip of the modiolus was opened, and a current-conducting and a voltage-measuring electrode were introduced into the opening. The resistance between the tip of the modiolus and the indifferent electrode was about 10,000 ohms. This value represents primarily the resistance of the nerve pathways and the blood vessels in the middle of the modiolus. As a next step, at a place about 8 mm away from the beginning of the basilar membrane, a hole was made through the wall of the vestibular scala to the modiolus, and the electrodes were introduced. The resistance from this point to the indifferent electrodes was 4200 ohms. The corresponding resistance for a length of the basilar membrane of 2 mm was 1300 ohms. The resistance fell to 150 ohms when the electrodes were placed in the internal meatus. This decrease in resistance is again a proof that the grounding resistances of the cochlea are along the pathway of the auditory nerve to the brain. In the measurement of the ratio of the two grounding resistances of the scala it was found that $R/R_1 = 0.43$ when an external generator was used to introduce the voltages at the stapes and the round window. If an external generator was not used, air-borne sounds were introduced into the cochlea, and its microphonic voltages were used for the measurement of the resistances. Then it was found that the ratio V_2/V_1 was about 0.12, where V_2 represents the voltage between the vestibular scala and the indifferent electrode and V_1 the voltage between the tympanic scala and the indifferent electrode. These two results seem to indicate that the cochlear duct with the endolymph, the cells of the organ of Corti, and the blood supply situated in the vestibular scala represent the main pathway for the current flow lines from the cochlea to the body of the guinea pig.

Voltage Attenuation along the Cochlear Partition. Let us assume that a voltage across the cochlear partition is produced at a place on the basilar membrane 1 mm from the round window, perhaps by microphonics. The question is how much this voltage is attenuated when it reaches the round window. It is of further interest to construct an electrical model for this voltage transmission. Two extreme situations are conceivable. It can be assumed that in the tightly coiled spirals of the cochlea the electrical insulation of the cochlear partition is very low, and that the whole inside of the cochlea is a homogeneously conducting body like a drop of fluid. Or it can be assumed that the cochlear partition insulates so well that the cochlea can be considered as a tube filled with fluid and separated into two canals by the cochlear partition. The electrical analog is a conducting cable. The problem is to determine which situation the cochlea more nearly resembles.

To obtain an estimate of the voltage drop in a homogeneous body, a metal trough about 2 cm deep was filled with physiological solution.

Needles plated with platinum black were immersed in this layer of fluid until the points touched the bottom of the trough. As the insert in Fig. 14-21 shows, the distance between the two electrodes of the generator was $2d$. The generator voltage was symmetrical with respect to the ground, so that there was an indifferent point halfway between the two generator electrodes. The voltage was measured between a movable electrode m and the indifferent electrode. If the angle in Fig. 14-21 was equal to zero, the voltage decrease was almost inversely proportional to the distance R . If, from the edge of the trough, a vertical insulating wall was moved toward the measuring electrode m , the voltage decrease with increasing distance was reduced as shown by the flattening

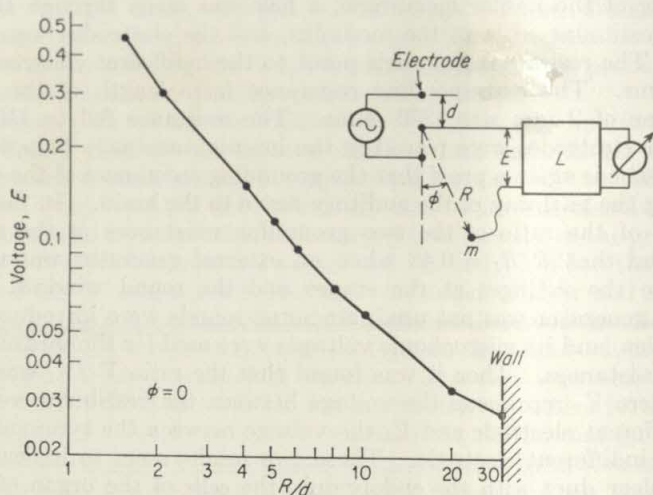


FIG. 14-21. Voltage drop in a homogeneous layer close to a dipole consisting of two parallel wires immersed in a shallow trough of water in a vertical position. The separation of the wires is $2d$. R is the distance between the two pickup electrodes connected to the amplifier.

out of the lower end of the curve in Fig. 14-21. If $R/d > 3$, the same voltage was obtained for all angles ϕ , so that for larger distances all the voltages approached zero (Attwood).

If a generator was connected to two parallel plates instead of to two needles, the voltage drop with increasing distance close to the electrode was relatively small, as shown in Fig. 41-22. For greater distances the voltage drop was again inversely proportional to the increase in distance.

For the dipole made from the parallel plates the voltage was greatest when $\phi = 0$ and was 0 when $\phi = \pi/2$. For a position of the measuring electrode m such that $R/d = 10$, the relative values of the voltage are given in Table 14-1.

TABLE 14-1

ϕ	0	15°	30°	45°	60°	75°	90°
Voltage.....	1.00	0.95	0.85	0.71	0.50	0.26	0

From these measurements it can be seen that, if two electrodes, insulated everywhere except at the tip, are introduced into a practically homogeneous medium, and if a voltage is impressed upon them so that a dipole results, then the voltage difference between two fixed measuring electrodes decreases as the distance is increased. For a given separation of the two measuring electrodes, this decrease with distance is much greater close to the dipole than farther away. Therefore the attenuation

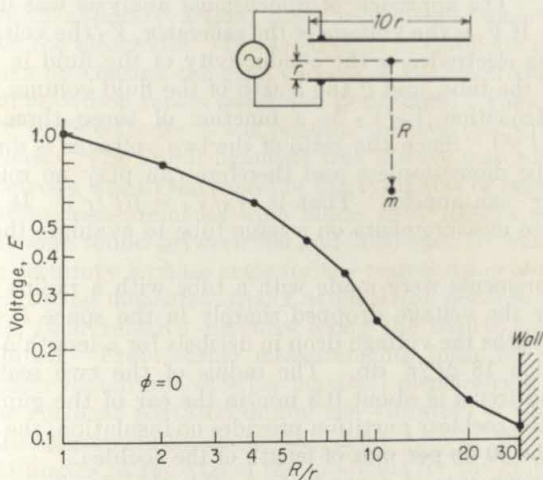


FIG. 14-22. Voltage drop in a homogeneous layer close to a dipole consisting of two parallel plates immersed in a shallow trough of water in a vertical position. The separation of the plates is $2d$.

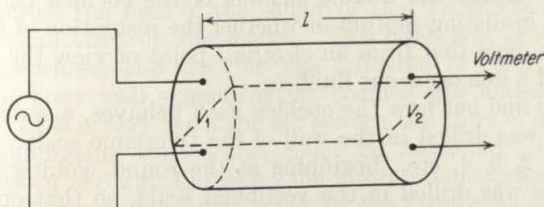


FIG. 14-23. Model for measuring the maximum voltage attenuation in a tube of conducting liquid.

of the voltage for a given separation depends upon the distance of the electrodes from the dipole.

In Fig. 14-23 the second extreme case is represented. The generator voltage is introduced at the left end of an insulated tube filled with fluid. On the right end are the measuring electrodes, in an insulated piston fitting inside the tube. If the cochlear partition is assumed to lie horizontally, as shown by the dotted lines of this figure, and if this cochlear partition has extremely high insulation, then as the length of the tube is increased there will be no appreciable drop in the voltage transmitted from the generator to the measuring electrodes. If the insulation is less,

however, the voltage will decrease with increasing length of the tube. Of special interest is the maximum attenuation that can be achieved when the cochlear partition provides no insulation, so that from the electrical point of view it simply does not exist.

Because it is difficult to construct a model with the same dimensions as the cochlea of a guinea pig, a large model was built, and the values for the normal size were calculated from the data obtained with the larger model. The approach of dimensional analysis was used for this calculation. If V_1 is the voltage of the generator, V_2 the voltage between the measuring electrodes, σ the conductivity of the fluid in the tube, r' the radius of the tube, and l' the length of the fluid column, we can say that the attenuation V_1/V_2 is a function of these three factors, or $V_1/V_2 = f(\sigma, l', r')$. Since the ratio of the two voltages is dimensionless, f also must be dimensionless and therefore can play no role, and only the ratio l'/r' can appear. That is, $V_1/V_2 = f(l'/r')$. It is therefore possible to use measurements on a large tube to evaluate the effect in a small tube.

The measurements were made with a tube with a radius $r' = 5$ mm. Consequently the voltage dropped sharply in the space $l' < 0.5r'$, but for greater lengths the voltage drop in decibels for a length $\Delta l'$ was given by the relation $18 \Delta l'/r'$ db. The radius of the two scalae together near the helicotrema is about 0.3 mm in the ear of the guinea pig, and therefore, if the cochlear partition provides no insulation, the attenuation along it can be 60 db per mm of length of the cochlea.

In the extreme case of a conducting cable the change in attenuation caused by the separation of the measuring electrodes is independent of their distance from the generator. Therefore, we now have a method for determining whether the double channel of the cochlea behaves like a tube with an insulating septum or whether the insulation of the cochlear partition is so poor that from an electrical point of view the cochlea can be considered a homogeneous fluid.

In order to find out how the cochlea itself behaves, a series of equally spaced holes was drilled in the wall of the tympanic scala. They were numbered 1, 2, 3, 4, etc., beginning at the round window. A similar series of holes was drilled in the vestibular scala, so that opposite each hole in the tympanic scala there was a corresponding hole in the vestibular scala. The voltage drop was recorded across the two measuring electrodes when they were moved from the No. 1 holes to the No. 2 holes. This voltage drop in decibels was found to be exactly the same whether the generator electrodes were inserted in the No. 3 holes or in the No. 6 holes. Therefore the cochlear canal behaves electrically, at least near the round window, exactly like a transmission line.

These measurements require meticulously clean surgical work, for if the surface of the cochlea is covered with mucus or fluid, the cross conduction from one electrode to the other depends on the position of the generator electrodes. An accumulation of fluid near the cochlea leads directly to the opposite extreme case, *i.e.*, zero insulation between the two scalae. Dental cement was not used because the cement never

adheres completely to the mucous layer covering the bony wall, and an accumulation of fluid under the cement can occur without being apparent. The best solution from the electrical point of view was to have the electrode wires standing free in the holes. For a distance 9 mm from the round window it was possible to show in precise measurements a transmission-line type of attenuation along the cochlear partition. Close to the helicotrema the distances between the electrodes were so small that, because of capillary action, there was always some fluid in the space between the electrodes. It was possible to eliminate this difficulty to some degree by coating the glass surface of the electrode with a thin layer of paraffin, which repels water and perilymph. Then by a proper positioning of the electrodes it was possible to force the perilymph back into the cochlea. The spiral ligament was always pierced so that the tip of the electrode was in the center of the tympanic or vestibular scala. The attenuation measurements were made with 100-cps currents, but no differences were found between 100 and 2000 cps. It was not possible to show with certainty a phase angle for the transmission of the voltages.

In addition to the measurements of attenuation between the different pairs of holes, their relative distances along the basilar membrane had to be determined. From earlier measurements (page 504), the points along the basilar membrane showing maximal displacement in the cross section of the cochlear partition during the vibration of the stapes had been plotted. Figure 12-21 shows the projection of this curve on a plane at right angles to the axis of the modiolus for the guinea pig. On the left side is the bony wall that connects the tip of the cochlea to the wall of the bulla. After the electrical measurements were finished the bulla was taken out, and the axis of the cochlea was pulled into a vertical position. Across the field of the ocular of the microscope there was a line with a small circle in the center. This circle was centered on the apex of the cochlea, and the line was adjusted to coincide with the middle of the bony wall supporting the cochlea (the dot-dashed line in the figure). In this way the angle ϕ between the pairs of holes and the bony wall supporting the cochlea could be measured. If imaginary radii were drawn through the holes, the intersection of these radii with the basilar membrane showed the point on the membrane to which each hole referred.

For the measurements of the attenuation along the cochlear partition a generator voltage was put into one of a pair of holes at a distance l mm from the beginning of the basilar membrane. Let us call the voltage for this position of the measuring electrodes V_1 , and let us call the measured voltage $V_{0.5}$ if the measuring electrodes were put in a pair of holes at a distance from the beginning of the basilar membrane $l = 0.5$ mm. In Fig. 14-24 the ratio of V_1/V_2 in decibels is given for different distances l along the basilar membrane. Attenuation along the cochlear partition did not show any remarkable change when the generator voltage was introduced in the No. 1 holes near the round window, and the attenuation values were measured in the holes toward the helicotrema.

Near the round window the cochlear partition has, in spite of the high attenuation, an appreciable insulation. For instance, at a distance $l = 5$ mm along the basilar membrane, the radius of the cochlear tube (tympanic scala and vestibular scala) is about 0.5 mm. The maximum attenuation could, therefore, be 18 db at a distance 0.5 mm along the

basilar membrane if the cochlear partition had no insulation. The measured attenuation had a value of about 3 db.

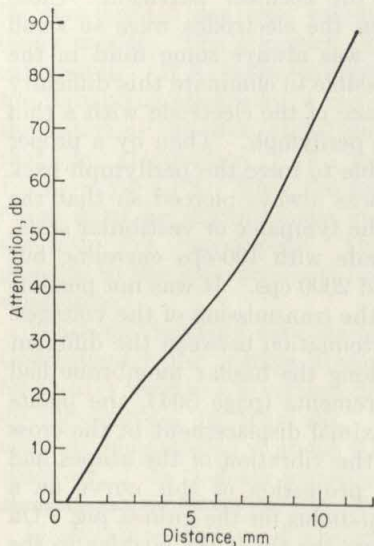


FIG. 14-24. Attenuation of a voltage across the cochlear partition as a function of distance along the cochlea, measured from a point 0.5 mm from the basal end of the basilar membrane.

Electrical Impedance of the Cochlear Tube. It was shown in the previous section that near the windows the cochlear tube (*i.e.*, the two scalae with the partition between them) can be considered as a transmission line, and the attenuation per millimeter of length of this transmission line can be measured. Therefore it should be possible to represent this electric transmission line by a resistance network. In Fig. 14-25a, for an element of length ΔL of the cochlear tube, the principal directions of current flow and the resistances in these directions are shown. This drawing bears some resemblance to the electrical model of the mechanical properties of the cochlea (Peterson and Bogert). For the elementary length of the cochlear tube ΔL , ρ_2 and ρ_1 represent the

longitudinal resistances of the vestibular scala and the tympanic scala, respectively. The transverse resistance of the cochlear partition is represented by r_0 , the resistances r_2 and r_1 are the grounding resistances of the two scalae, and ρ_0 represents the resistance of the grounding pathway, that is, the internal resistance of the nerve and blood vessels in the modiolus. In addition to these resistances, we must assume that every section ΔL has resistances Ω_1 , Ω_2 , etc., which lead from one section to another, because there is no complete insulation between the different parts of the cochlear winding. According to the theory of transmission lines the complicated resistance network of Fig. 14-25a can be represented by the simple circuit of Fig. 14-25b. As indicated for a given length ΔL of the basilar membrane, the attenuation ratio of the transverse voltages $K = V_1/V_0$ can be measured. Furthermore it is possible to determine the longitudinal resistances ρ of the cochlear tube, but it seems to be very difficult to measure the insulation (shunt) resistance r of the cochlear partition, because in such a measurement the current flow lines must be perpendicular to the cochlear partition, which is difficult to achieve with measuring electrodes having a small point. An important

electrical value of the cochlear tube is the characteristic impedance Z of the transmission line because it represents the loading resistance across the cochlear partition. It is well known that for a transmission line

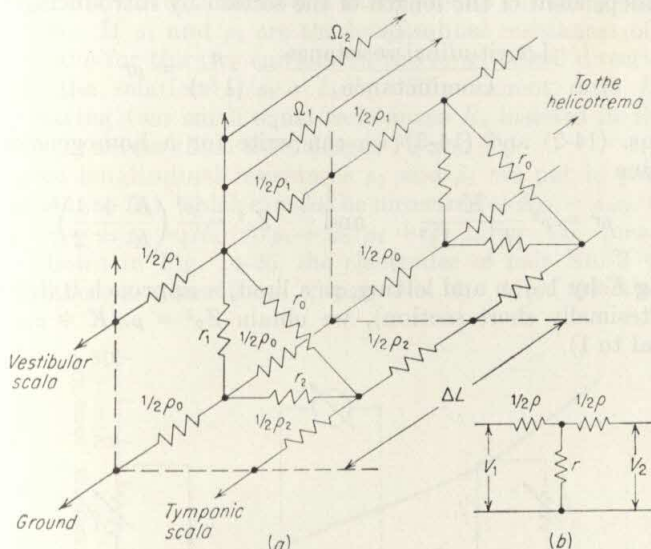


FIG. 14-25. (a) A schematic drawing of the resistances in a section of length L of the cochlear duct and (b) its electrical equivalent.

of the form represented in Fig. 14-25b we have (from Markus and Vin Zeluff)

$$r = \rho \frac{K}{(K - 1)^2} \quad (14-2)$$

$$Z = \frac{\rho}{2} \frac{K + 1}{K - 1} \quad (14-3)$$

According to this formula the characteristic impedance Z depends upon the length ΔL of the section considered. The cochlea represents a completely continuous line, and therefore it seems to be reasonable to make the sections as small as possible. For the attenuation in nepers (1 neper = 8.7 db) we have

$$K = \frac{V_i}{V_0} = e^n = 1 + \frac{n}{1!} + \frac{n^2}{2!} + \dots$$

which for small n converges toward $1 + n$. If D represents the attenuation for an element of length ΔL of the cochlear partition measured in decibels, then for a section on the cochlear partition with a length L , $K = 1 + 1/8.7 \times DL$. If we consider the longitudinal resistance per unit of length of the cochlear partition, $\Omega = \rho/\Delta L$. If this value is introduced into Eq. (14-3), we have for the impedance of the homogeneous transmission line (as ΔL approaches zero) $Z_0 = 8.7\Omega/D$. The longitudinal

resistance ρ increases in proportion to the length of the section considered. In the same way the conductance across the cochlear partition increases in proportion to the length of the section. We have therefore a value that is independent of the length of the section by introducing the ratio

$$\frac{\text{Longitudinal resistance}}{\text{Conductance}} = \frac{\rho}{(1/r)} = \rho r$$

From Eqs. (14-2) and (14-3) we can write for a homogeneous transmission line

$$\rho r = \rho^2 \frac{K}{(K-1)^2} \quad \text{and} \quad Z_0^2 = \frac{\rho^2}{4} \left(\frac{K+1}{K-2} \right)^2$$

Replacing K by $1+n$ and letting, as a limit, n approach 0 (for we have an infinitesimally short section), we obtain $Z_0^2 = \rho_r/K \doteq \rho_r$ (as K is here equal to 1).

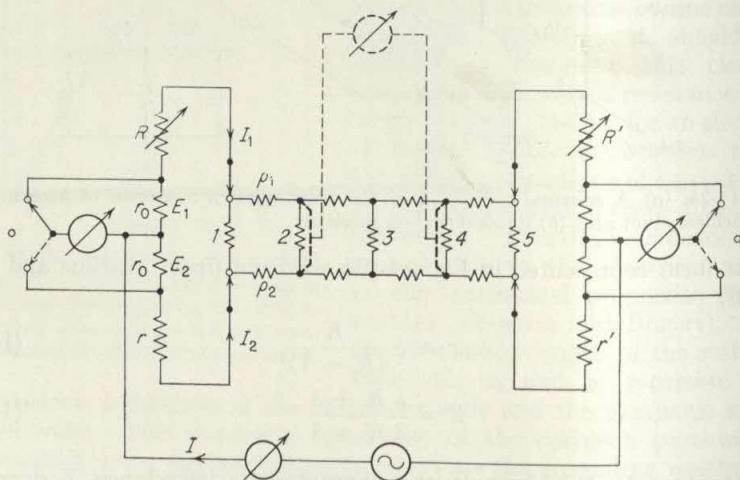


FIG. 14-26. Bridge for separate measurement of the longitudinal resistances of the tympanic and vestibular scalae.

To determine the impedance the next step was to measure the longitudinal resistance of a length Δl of the cochlear partition. In the schematic network represented in Fig. 14-25b, ρ is the sum of the longitudinal resistances in the vestibular scala and the tympanic scala (ρ_2 and ρ_1 in Fig. 14-25a). A study of histological cross sections of the cochlea of the guinea pig made it clear that the cross sections of the two scalae are different. Therefore the longitudinal resistance ought to be measured for each scala separately. This can be done, of course, only if it is possible to prevent a flow of current through the cochlear partition during the measurements, which can be achieved in some degree by placing the cochlear partition in the middle of a Wheatstone bridge. The wiring diagram for this sort of measurement is shown in Fig. 14-26.

Five pairs of electrodes were introduced along the cochlear partition, and the resistances R , r , R' , and r' were adjusted so that the electrode pairs No. 2 and No. 4 showed no voltage difference. Therefore, at the locus of electrodes No. 2 and No. 4 there was no current going through the partition. If ρ_1 and ρ_2 are the longitudinal resistances of the two scalae, we have for the two currents in the longitudinal direction of the two scalae the relation $\rho_1/\rho_2 = I_2/I_1$. The current ratio I_1/I_2 was found by having two small equal resistances R_k inserted in the circuit and measuring across them the voltages V_1 and V_2 .

If the two longitudinal resistances ρ_1 and ρ_2 are put in parallel, we get the resistance $R_{\Delta l}$, which can also be measured as $R_{\Delta l} = \rho_1 \rho_2 / (\rho_1 + \rho_2)$. Hence $\rho = \rho_1 + \rho_2 = R_{\Delta l}(\rho_1/\rho_2 + \rho_2/\rho_1 + 2)$. For the measurement of $R_{\Delta l}$ as shown in Fig. 14-26, the electrodes of pair No. 2 were connected together, as were those of pair No. 4. After this the voltage

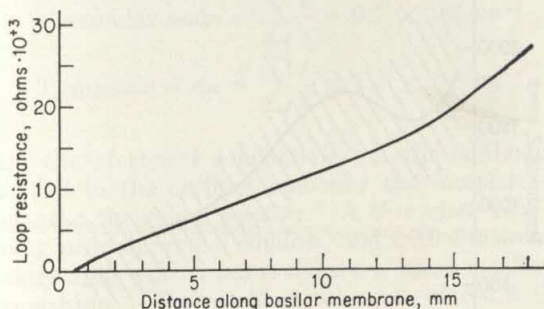


FIG. 14-27. Loop resistance of the cochlea as a function of distance along the basilar membrane.

difference between electrode pair No. 2 and electrode pair No. 4 was measured at the same time with the whole current I going through the bridge. Ohm's law gives the resistance $R_{\Delta l}$. This is a potentiometric measurement, and the resistance of the electrodes plays no role. Close to the round window the longitudinal resistance of the vestibular scala ρ_2 is in general 1.5 to 2.5 times larger than ρ_1 . The reason for this is that near the round window the cochlear tube is wound almost completely around the edge of the round window. This sharp turn increases the length of the vestibular scala and decreases the length of the tympanic scala. About halfway between the window and the helicotrema this ratio is reversed, because the tympanic scala has a smaller cross section than the vestibular scala. These large variations in the value of ρ made it necessary always to make the measurements for small sections and then to add them together. The No. 3 holes were used for this purpose.

In Fig. 14-27 the sum of the two longitudinal resistances is given for different distances along the basilar membrane. Disregarding some small irregularities at the beginning of the basilar membrane, the longitudinal resistance increases from the window almost proportionally with the length to a distance of about 13 mm. Close to the helicotrema we

are really measuring only the longitudinal resistance of the tympanic scala, because the vestibular scala shrinks to a small round globule.

From the attenuation curve of Fig. 14-24 and the longitudinal resistance curve of Fig. 14-27 the impedance of the cochlear tube can be calculated for different places. In general the impedance was determined by measuring simultaneously the attenuation for two given electrode pairs and the corresponding longitudinal resistances. The values for the impedance for different lengths of the basilar membrane are shown in Fig. 14-28.

The above considerations are valid for a voltage attenuation across the cochlear partition. From Fig. 14-25 we can see that the ground acts like the sliding contact of a potentiometer between the two scalae. Therefore we expect that a voltage between one of the scalae and the

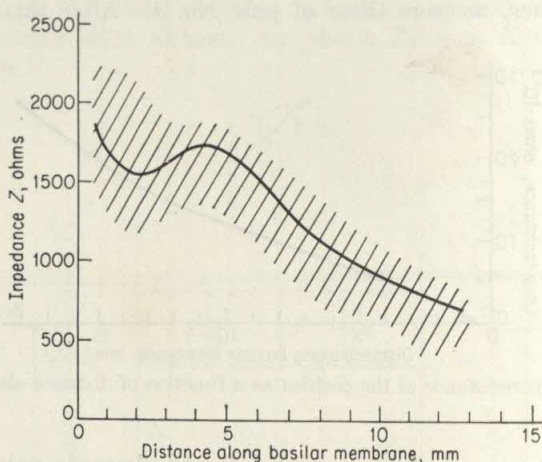


FIG. 14-28. Transmission impedance of the cochlear duct as a function of distance along the basilar membrane, measured from the round window. The crosshatching indicates the variability of a group of twenty guinea pigs.

ground is attenuated along the cochlear partition in about the same way as the voltages across the cochlear partition. This can be proved experimentally to some degree if the necessary precautions are taken and if the ground capacitance of the generator is small.

If in one of the scalae a voltage is introduced in the longitudinal direction, for instance by putting two electrodes in the vestibular scala about 0.2 mm apart from each other, then a local current loop is introduced. This produces a voltage difference across the cochlear partition, which is attenuated along the partition in the same way as that described above.

It is of interest to determine whether the longitudinal resistances ρ_1 and ρ_2 in Fig. 14-25a are the resistances of the perilymph columns in the scalae or whether other factors are involved. From Fig. 14-27 we can see that the loop resistance from the stapedial footplate to the helicotrema to the round window has a value of about 30,000 ohms. We are able to

calculate the resistance of the perilymph column from the cross-sectional areas of the two cochlear scalae.

The electrical resistance of a fluid column is calculated by the formula

$$R = \frac{l}{s} \frac{1}{\sigma_{fl}}$$

where σ_{fl} represents the electrical conductivity of the perilymph and l the length of the tube with a cross-sectional area of s . The value of l/s was determined from microscopic cross sections of the cochlea of the guinea pig. From the map of the cochlea shown in Fig. 12-21 the positions of the microscopic cross sections were determined, as were the lengths of the different sections with given cross-sectional areas s . For the whole length of the two scalae we obtain

$$\text{Vestibular scala} = \sum \frac{l}{s} = 0.7 \times 10^3 \text{ cm}^{-1}$$

$$\text{Tympenic scala} = \sum \frac{l}{s} = 1.1 \times 10^3 \text{ cm}^{-1}$$

To measure the electrical conductivity of the perilymph, two little holes were drilled in the cochlea, one near the footplate of the stapes and the other near the round window. A thin glass tube was inserted into the opening near the round window, and with a micrometric syringe a drop of perilymph was withdrawn into a glass capillary tube with uniform cross section. This capillary tube was placed horizontally and kept at a constant temperature of 37°C. An electrode made of Taylor wire was inserted into each end of the tube. The change in resistance was measured as the two electrodes were brought closer together. The radius of the capillary was 0.47 mm, and the resistance of the fluid column was 725 ohms per mm. Therefore the conductivity of the perilymph at 37°C is $\sigma_{fl} = 2 \times 10^{-2}$ mho per cm.

It was possible to suck out only one drop of fluid from the cochlea, and the handling of this drop was sometimes difficult. It was important to have the capillary in a humidity chamber with a physiological solution as the humidifier so that the perilymph did not evaporate and change its conductivity. The vapor tension of the perilymph and the physiological solution is not the same, which made it necessary to carry out the measurements as quickly as possible. It was sometimes startling to see that when the electrodes were inserted into the ends of the capillary tube, the drop of perilymph simply disappeared from the tube. The reason for this was that the insertion of the electrode reduced the cross-sectional area of the tube at that point, and the capillary forces sucked the drop from the tube. This difficulty could be overcome by putting a thin coat of paraffin on the electrodes so that the insertion of the electrodes forced the perilymph into the tube.

From the values obtained it was possible to calculate the loop resistances of the two scalae. For the perilymph a value of about 110,000

ohms was obtained, which is four times larger than the measured loop resistances. This discrepancy can be explained by assuming that the cochlear partition is filled with a fluid with better electrical conductivity than the perilymph, but the main explanation is that the grounding resistances ρ_0 in Fig. 14-25 play an important part as well as does the conductivity between different sections of the cochlea. These conditions greatly reduce the longitudinal resistance of the cochlear tube.

The closer we come to the helicotrema, the smaller are the insulations between the different turns, and near the helicotrema we can no longer consider the cochlear tube as a transmission line. In the last turn one scala becomes a globe. Therefore, in this part of the cochlea the attenuation of voltages is the same as in a drop of fluid.

MICROPHONICS PRODUCED BY TOUCHING THE COCHLEAR PARTITION WITH A VIBRATING ELECTRODE*

Earlier studies showed that a sinusoidal vibration or a sudden displacement of the stapedial footplate produces a spatially damped wave that travels along the cochlear partition toward the helicotrema. This vibratory pattern is highly complicated, and its investigation is made particularly difficult by the fact that some parts of the cochlear partition are moving upward while other parts are moving downward. Most measurements of potential in the cochlea represent an integration of voltages produced along a length of the cochlear partition, and are difficult to interpret.

A reasonable solution seemed to be to touch one point on the cochlear partition with a sharp vibrating needle so that only a small section would be set in motion, with all its parts in phase. As will be seen, this approach has both pitfalls and successes.

Uncertainty of Physical and Physiological Observations. As every physicist knows, an ammeter inserted into an electric circuit alters the current distribution. The introduction of the measuring equipment produces uncertainty. Sometimes this uncertainty can be eliminated by further measurements, as by a consideration of the impedances of the electrical network and the ammeter when only the magnitude of the effect has been influenced by the measuring device. With neurophysiological systems matters are usually more complex. Such systems are often stimulated in several different ways. If one path is blocked, another may take its place. Thus we may seem to have a completely normal function, though the measuring equipment may have brought about a change not only in the magnitude but even in the pathway of the neural action. Because the usual pathway has been blocked, abnormal conditions have been produced. For example, muscle fibers ordinarily are excited in a random fashion. But if a muscle contraction is elicited by an electric shock applied to a motor nerve, all the individual muscle fibers contract instantly and at the same time. Such a contraction does not ordinarily occur in a living animal.

* Article 60 as listed in the Author's Bibliography. Published in 1951.

In the following experiments the intention was to keep all the stimulations of normal type and magnitude. In an attempt to define the type of stimulation to be considered normal, a study was made of the blood supply in the capillaries of the ear. When the bulla is opened the internal surfaces are seen to be pale pink in color. Under a stereoscopic microscope with a magnification of 150 times, the red blood corpuscles may be seen in the capillaries, and their velocity of movement provides a measure of the blood supply. If the surface of the cochlea is touched with a hair, there is a sudden change in the pattern of the blood supply, even in areas far removed from the point of the pressure. The diameter of some of the capillaries is increased two or three times, while in other capillaries all movement of the corpuscles suddenly ceases.

After study had established the normal pattern of movement in the capillaries, preliminary experiments were carried out to determine how best to maintain normal physiological conditions during an operation. It was clear that the environs of the animal must be kept at normal body temperature. To do so, all the instruments and the microscope were mounted on a steel leveling plate as shown in Fig. 14-29. The temperature of this plate was kept 0.5°C above the body temperature of the animal to prevent moisture from the saturated air of the middle ear and the wound from condensing on the instruments and microscope lenses. All the surgical instruments were kept on the heated plate so that they would be at body temperature when they were used. The cochlea of the guinea pig is so small that even a thin metallic needle can cool it. Fortunately the blood supply to the inside of the cochlea comes from the brain, and the streaming velocity of the corpuscles remains normal longer in the capillaries inside the osseous spiral lamina than on the surface of the cochlea.

Numerical data are available on the normal range of displacement and vibration of the cochlear partition relative to the cochlear wall. Earlier measurements (page 173) made on the human ear showed that for sound pressures in the external auditory meatus close to the threshold of feeling the vibratory amplitude of the cochlear partition is of the order of 10^{-4} cm in the frequency range between 500 and 3000 cps. A contact with the cochlear partition that produces a displacement of this order of magnitude is tolerated just like a normal acoustic stimulus. Experience has shown that a displacement as much as three to five times greater than this does not produce any lasting changes in the cochlear partition when the displacement is made slowly, over a span of 0.1 sec.

These values set the requirements for the micromanipulators and for the vibrations between the instruments and the cochlear partition. It is obvious that the whole operating table had to be shock-mounted to reduce vibrations from the floor. The microphonics seem to be fairly insensitive to anesthesia as long as the local blood supply is not altered.

Vibrating Electrode. In order to set a single point on the cochlear partition into vibration and at the same time to record the generated microphonics with maximum sensitivity, the vibrating needle was combined

with an electrode. This simplified the measuring procedures, because only one needle had to be introduced into the cochlea.

Confining the measurements on the cochlear partition to a small section has the advantage that, if by accident the cochlear partition is destroyed by the vibrating electrode, it is only necessary to move it to a new location, and the making of a completely new preparation is not required.

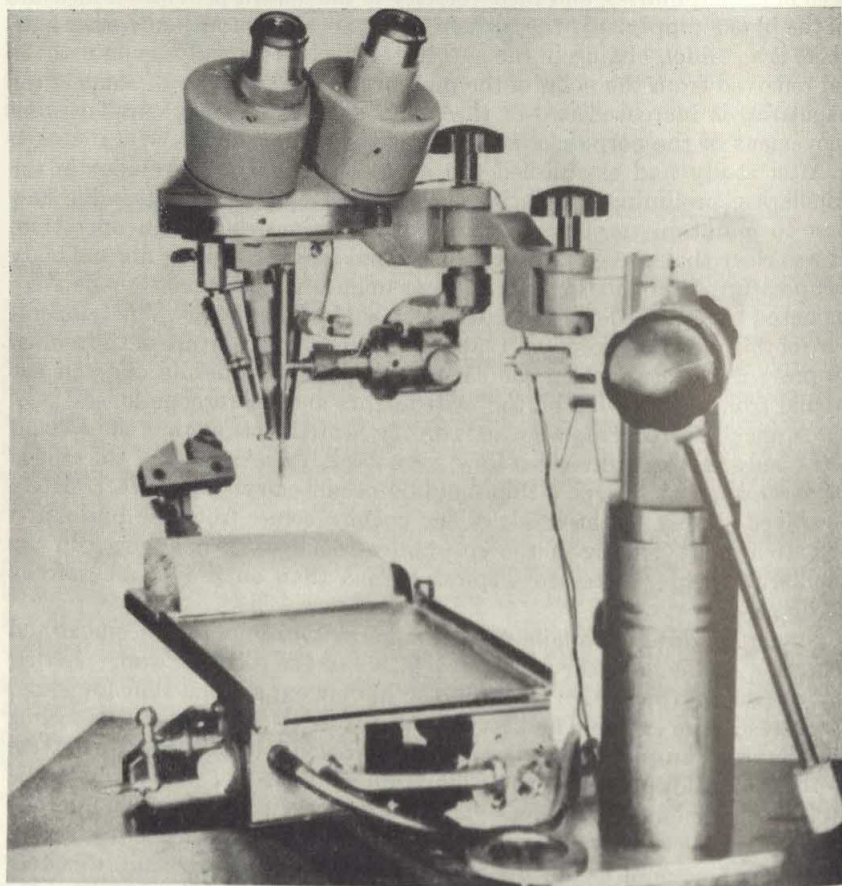


FIG. 14-29. Equipment for measuring cochlear microphonics.

Unfortunately the maximum tolerable vibration of the instrument is so small that it was necessary to have a highly stable and complicated set of adjustments, as shown in Fig. 14-29.

In the preliminary trials the basilar membrane was touched with a simple electrode with the aid of a micromanipulator. It was possible to observe the microphonics produced by moving the electrode in any of three orthogonal directions: radially (across the partition), longitudinally (along the length of the partition), and vertically (up and down relative to the partition). The micromanipulator, shown in Fig. 14-30, con-

sisted of the needle *N*, the body *B*, and the handle *H*, fixed on the objective of the microscope. The tip of the needle is in the middle of the field of view and can be seen clearly. The screw *S* makes it possible to put the manipulator into position with one twist. The movements of the handle *H* were transmitted to the electrode end in a ratio of about 1:100.

The magnification of the microscope was 150 times. The cochlear partition was usually covered with perilymph, and the depth of the fluid sometimes varied a great deal. It therefore was necessary to equip the

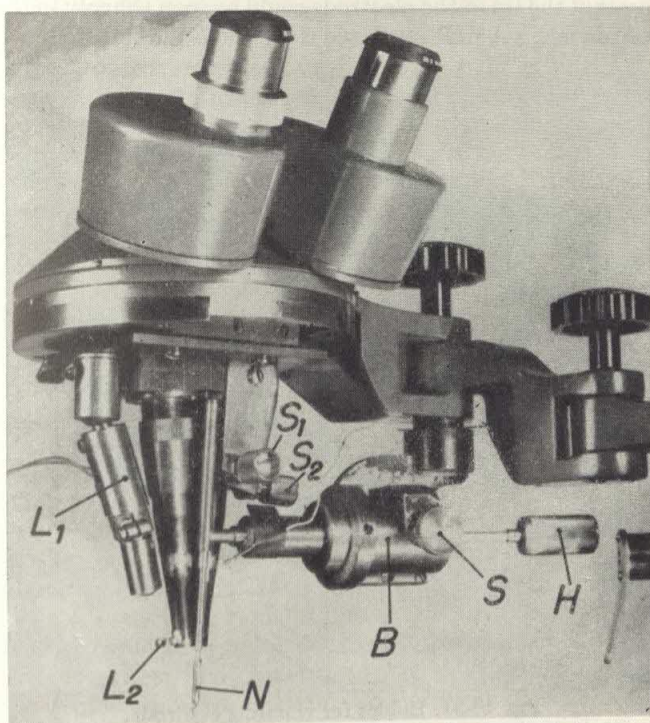


FIG. 14-30. Method of mounting the micromanipulator.

objective with two screws, *S*₁ and *S*₂, so that the two stereoscopic images could always be combined. The screw *S*₂ adjusted the distance of the microscopic image from the eye. If the distance of the image was the same as that of the preparation, working under the microscope was made considerably easier. Sometimes it was even possible to use the instruments freehand and to bring them into the field of view with a high degree of accuracy.

For coarse horizontal adjustments the microscope was mounted, as shown in Fig. 14-29, on a precisely ground horizontal steel plate that could slide smoothly on the leveling plate. A layer of grease between the two plates provided enough adhesion to keep the microscope in place. The compound cross slide of a watchmaker's lathe provided the small horizontal movements of the operating table. The usual coarse vertical

adjustment on the microscope is very tiring to the hands, because the small depth of focus makes it necessary to move the microscope up and down constantly. On the other hand, if these adjustments are not made precisely, it is very tiring to the eyes. Therefore the knob was equipped with a lever about 30 cm long, as shown in Fig. 14-29 and described on page 36. This improvement reduced the operating time appreciably.

The construction of the vibrating electrode is shown in Fig. 14-31. It consisted of a slide *S* that was fitted on the objective of the microscope in such a way that the tip of the electrode could be seen sharply in the middle of the field of view. A well-insulated electrode *E* was located in a tube *T*.

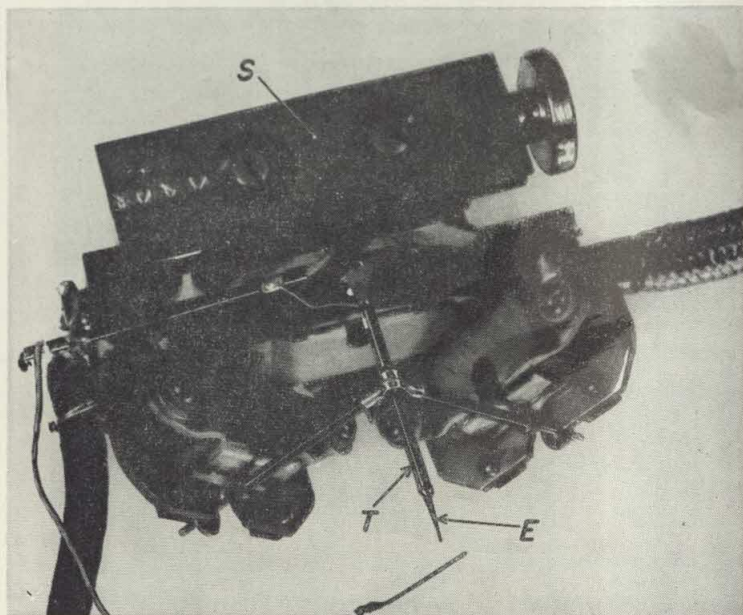


FIG. 14-31. Holder for vibrating electrode.

A wire was connected to the indifferent electrode. Three magnetic driving units were fixed in such a position that tube *T* could be moved in the three directions of the coordinate system. With sinusoidal currents it was possible to vibrate the point of the needle in any direction by introducing a phase difference between the different vibrating systems. It was even possible to make the tip of the electrode rotate in a circle.

Stroboscopic illumination showed, under the microscope, that the vibrations of the tip of the electrode corresponded in values and directions to those for which the apparatus was set.

Artifacts. The vibrating electrode proved to be a powerful tool for determining what types of living tissue are capable of producing microphonics. If the surface of a physiological solution was touched with the vibrating electrode and an indifferent electrode was measured, voltages of a few microvolts could be detected. If blood serum was collected in a cavity

in the living animal and the electrode was placed in this pool, the resulting voltages between this electrode and the indifferent electrode were very small. The surface of a freshly cut muscle also gave only a few microvolts. Even the surface of the auditory nerve and various parts of the brain did not produce large voltages. But if the wall of the cochlea was opened and contact was made with the perilymph-air boundary, voltages between this point and an indifferent electrode often gave values as great as 100 to 300 μv . It was not an easy task to discover whether this voltage was produced on the surface of the perilymph or whether it was produced by microphonics resulting from the transmission of the surface movements to the cochlear partition.

Lippmann has shown that the deformation of a mercury-air boundary produces voltages. The same was shown to be true for the perilymph-air boundary. For this purpose a drop of the perilymph of the cochlea was allowed to flow into the cavity of the bulla. The indifferent electrode was placed on the edge of the drop, and a measuring electrode was immersed in another part of the drop. If now the surface of the drop was touched with a thin glass rod so that a small deformation of the surface could be seen under the microscope, a large voltage spike was produced. Since the boundary between blood serum and air does not produce this type of spike, from the point of view of electrocapillarity the perilymph of the cochlea must be regarded as a special type of fluid.

Unfortunately the opening of the cochlea and the introduction of an electrode not only produces a boundary between the perilymph and air, but at the same time produces boundaries between the perilymph and the metal of the electrode and between the electrode and the air. Thus the voltage situation, especially the direct voltage, is highly complicated.

Besides the electrocapillarity other artifacts are to be expected from the streaming of the fluid. Thus Helmholtz (3) found that the voltage between two electrodes increases if one of them is in a moving stream of fluid. It is well known that the voltage of a Daniell's cell changes if one of the electrodes is moved (Procopiu). This kinetic feature of voltage production seems to be present in the perilymph also. An electrode coated with platinum black and moved in a physiological solution does not produce high voltages, but if some cotton is immersed in the physiological solution, the kinetic voltages rise to as much as 10 to 50 μv . The displacement of fluid along a fluid-gas boundary without deformation of the surface can give rise to a voltage, as was shown by Quincke. Kupfer discussed the production of microphonics in connection with some of these phenomena.

In the experiments described here these artifacts were sometimes so large that at first it was difficult to separate them from the voltages produced by the cochlear partition. Some of the electrocapillary voltages of the perilymph were even found to decrease under oxygen deprivation and upon the death of the animal, much as do the microphonics, though usually somewhat more slowly.

In spite of these difficulties it was possible to show that the contact between the basilar membrane and the vibrating electrode produced

voltages. For this purpose the vibrating electrode was made to touch the basilar membrane close to the round window, where the basilar membrane is stiffest and where a small displacement of the electrode caused a large increase in the tension of the membrane. If a small hole was made in the round-window membrane and the visible part of the basilar membrane was placed in a horizontal position, and if care was taken that the perilymph did not escape but continued to form a deep layer on the basilar membrane, the insertion of the vibrating electrode showed the following effects (for these investigations a convenient frequency was 50 cps). At the moment the electrode touched the surface of the perilymph a large voltage arose between the electrode and an indifferent electrode. If the electrode consisted of a free platinum wire coated with platinum black, dipping the electrode into the fluid decreased this voltage. By going still deeper it was observed that a vibratory amplitude of even less than 0.01 mm could give rise to an alternating voltage of the same frequency as that of the electrode. This alternating voltage was greatest if the basilar membrane was touched just beneath the cells of Corti. If it was touched close to the spiral ligament, the voltage was less. If the bony wall of the cochlear partition was touched, no voltage was usually picked up. If the tip of the electrode was pushed deeper into the basilar membrane, a further small increase of the voltage could be obtained, but soon the voltage decreased, and it practically disappeared when the cochlear partition was pierced through. The voltage was always largest when the tip of the electrode just touched the basilar membrane. This observation could be verified by sucking away the perilymph so that under a binocular microscope the position of the electrode relative to the basilar membrane could be seen more exactly.

If, while the electrode was touching the basilar membrane, the membrane was cut through at points 0.7 mm on either side of the electrode, the microphonic voltage was maintained for about 5 sec. This showed that the vibrating strip of membrane was responsible for the microphonics. After 5 sec the microphonic voltage declined because the blood supply to the isolated strip was inadequate.

A problem of a different nature is raised by the question whether the movements of the fluid in the cochlea are transmitted to the vestibule so that microphonics are produced in the utricle and saccule. The saccule of the guinea pig is a thin chalky white layer, like a veil. When this veil was touched with the vibrating electrode it was usually destroyed instantly. It was therefore impossible to determine whether the saccule could produce microphonics. On the other hand, the utricle has a well-cushioned triangular plate, which can be displaced in any direction without any apparent changes in its structure. When this plate was touched with the tip of the vibrating electrode, microphonics were produced that were similar in all respects to the microphonics observed on the basilar membrane.

Fortunately, it is possible to show that the voltages produced by touching the basilar membrane with the electrode are not produced by vibrations of the utricle transmitted hydrodynamically from the basilar

membrane to the utricle. If the maximum voltages occurring on the basilar membrane were measured near the round window, it was possible to show that the value of these voltages did not change when the stapes was extracted from the vestibule. Then the fluid movements produced by a displacement of the basilar membrane were no longer transmitted with the same amplitude to the utricle. Even the destruction of the utricle did not alter the microphonics on the basilar membrane. But this last experimental result is less definitive, because it was impossible to determine whether all the sensitive parts of the utricular end organ had been destroyed, especially when an effort was made to avoid a great deal of bleeding. In another experiment cotton was introduced into the vestibule and pressed against the utricular plate so that the utricle was under constant maximum stimulation. Then no further increase in voltage was produced by the movements transmitted from the basilar

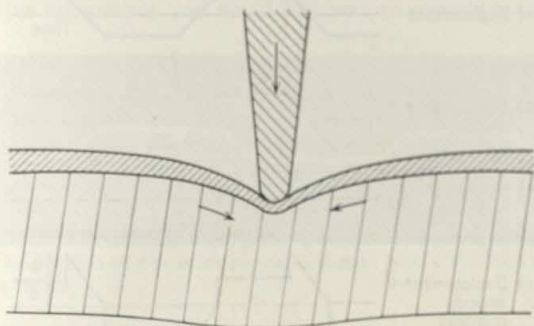


FIG. 14-32. Effect of the pressure of a needle on a double-layered membrane.

membrane. These experiments give further evidence that the microphonics are produced by the cochlear partition.

Figure 14-32 shows an elastic membrane consisting of two different layers, the upper of which is stiffer than the lower. If the tip of a needle is pressed against such a membrane, the softer parts are pushed against the tip of the needle as indicated by the arrows of the figure. If instead of pressing near the center of the membrane we press near one edge, there will be produced in the inner part of the membrane a horizontal displacement toward the needle. If the needle is moved to the opposite edge of the membrane, the direction of the displacement inside the membrane will be reversed. Therefore, if the microphonics are produced by these internal displacements, their phase ought to depend on which edge of the membrane is stimulated. This hypothesis was tested with a needle whose tip had a diameter of 0.01 mm and which vibrated at 200 cps. Although the phase reversal was not obtained on every trial, it was observed several times, and this evidence indicated strongly that the microphonics are produced inside the cochlear partition.

If the footplate of the stapes is vibrated by air-borne sounds in a normal middle ear, large masses of perilymph are moved in the vestibule in the immediate vicinity of the utricle. It will be necessary to carry out

special investigations to determine to what extent the utricle can contribute to the microphonics picked up at the round window under these conditions.

Relation of the Microphonics to Displacement, Velocity, and Pressure.

A comparison of many different elastic materials gives the impression that hard materials generally exhibit purely elastic properties, but soft materials exhibit an internal viscosity and show aftereffects following deformation. On the other hand, earlier measurements proved that for small vibrations the soft structures of the cochlear partition follow Hooke's law (page 464): a force acting on the cochlear partition produces a proportional deformation. In other words, displacement is proportional to pressure, and in considering the origin of the microphonics we can confine our attention to one of these two variables.

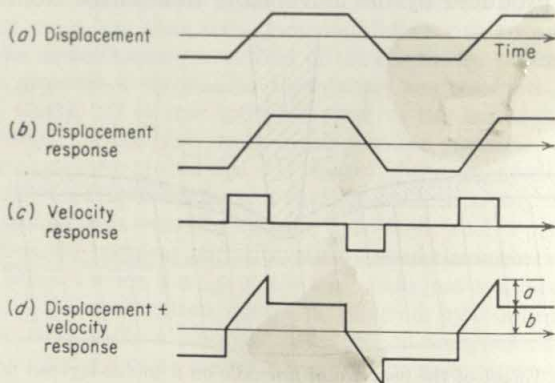


FIG. 14-33. (a) Waveforms of the stimulus and (b), (c), and (d) possible forms of microphonic response.

Because it is to be expected that the elastic properties of the cochlear partition are different at different places and may change with time, a method was developed to show immediately whether the microphonics are proportional to the magnitude or to the velocity of the deformation. For this purpose the upper and lower peaks of an alternating sinusoidal current of about 20 cps were clipped, so that the waveform of the current through the vibrator was trapezoidal, as illustrated in curve *a* of Fig. 14-33. Now, if the microphonic voltage is proportional to the displacement, it will have the shape shown in curve *b*. But if the microphonics are proportional to the velocity of the displacement, rectangular pulses will occur like those shown in curve *c*. If, on the other hand, the microphonics depend on both the displacement and the displacement velocity at the same time, the voltage will have the form of curve *d*. Also in curve *d* the ratio between parts *a* and *b* would enable us to determine the ratio between the microphonic voltages produced by the displacement and those produced by the displacement velocity.

With the vibrating electrode on the basilar membrane near the round window in a fresh preparation, clear trapezoidal waves were always

obtained for vertical and for radial displacements, as shown in the oscillogram of Fig. 14-34. These microphonics are therefore proportional to the displacement. But when the vibrating electrode was placed on Reissner's membrane near the helicotrema, a small velocity component was always found. Its magnitude was 10 to 20 per cent of that of the displacement component. A local displacement of Reissner's membrane is therefore partially transmitted to the deeper parts by frictional forces.

If the vibrating electrode was applied to the footplate of the stapes, the velocity component was overwhelmingly large. It was possible to show also that abnormally large amplitudes of vibration act so as to loosen the internal structure of the cochlear partition and sever the elastic connections between its parts. Thereafter the displacements are produced by frictional forces. The observation of the velocity component is a very sensitive technique and could be used to ascertain what values of

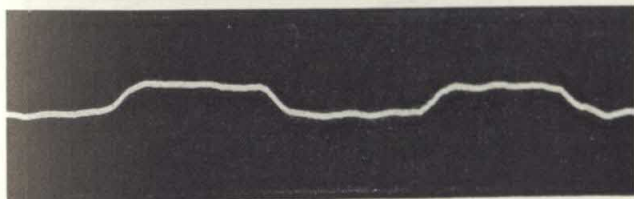


FIG. 14-34. Oscillogram of the microphonic response to the stimulus shown at (a) of the preceding figure.

vibrating amplitudes loosen the internal structure of the cochlear partition. By testing along the cochlear partition even local damage could be detected.

The fact that trapezoidal displacements of the electrodes produce trapezoidal microphonic voltages on the basilar membrane is evidence that a displacement of the cochlear partition with sharp needles does not produce microphonics in the utricle, because the utricle can be stimulated only by movements of the fluid, and these movements would produce a velocity component.

From the trapezoidal form of the voltage it was observed that the voltage lasts as long as the deformation. The question is, for how long a period of time will this continue to be true? This matter is of great interest because a continuous microphonic voltage produces a continuous current and represents a continuous energy consumption. Unfortunately it was difficult to measure the voltage between an indifferent electrode and an electrode touching the basilar membrane with a constant pressure over a long period of time. Even when conditions were kept as constant as possible, the base line of this voltage showed a continual wavering produced by breathing and by small changes in blood supply and body temperature. For periods of 1 to 2 sec these changes did not disturb the base line too seriously. The upper part of Fig. 14-35 shows the microphonic voltages produced by sudden displacements of Reissner's

membrane close to the helicotrema at intervals of 1.3 sec. The lower figure shows the microphonics produced by displacements of the basilar membrane near the round window.

If the preparation was fresh a constant static deformation on the basilar membrane produced a direct voltage that remained constant for several seconds. If the oxygen supply to the animal was diminished or the cochlea was cooled, or if the amplitude of the vibrating electrode was made so great that mechanical changes were produced inside the cochlear partition, the voltage did not remain constant but decreased after every sudden displacement. A decrease in the oxygen supply not only decreased the value of the direct voltage but also caused it to fall more rapidly. With a high degree of oxygen deprivation the voltage dropped to half its original value within 0.01 sec after the displacement had been made.

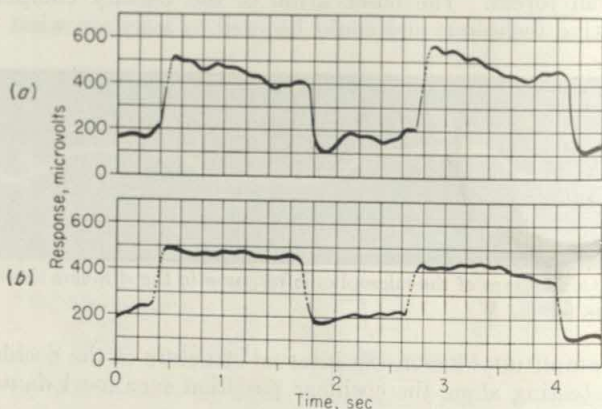


FIG. 14-35. Graphs of the cochlear microphonics resulting from stimulation with an electrode producing a sudden displacement of Reissner's membrane, (a) at a position near the helicotrema and (b) at a position near the round window.

A displacement of Reissner's membrane near the helicotrema always showed a slow decline in the voltage, even in good preparations, as can be seen in the upper curve of Fig. 14-35. This drop presumably resulted from some viscous forces operating within the cochlear partition. Vertical movements of the electrode produced microphonic voltages up to 1 mv. Even for these large values the voltage was still proportional to the magnitude of the displacement.

Relation of the Microphonics to the Direction of the Displacements. As shown in Fig. 14-32, every displacement of an electrode vertical to the plane of the basilar membrane produced displacements of the internal portions of the cochlear partition in the plane of the basilar membrane. Therefore precise discrimination among the displacements in the three coordinate planes was not possible. However, an approximate judgment of the most sensitive direction could be made with the vibrator shown in Fig. 14-31. As the impedance of the cochlear partition for displacement in its own plane depended to a high degree upon the depth to which

the needle was inserted, it could not easily be measured. For this reason no measurements were made of the sensitivity to displacements in different directions for a given pressure of the needle point. The measurements were made instead for a given magnitude of displacement of the tip in each of the three directions. The point of the electrode was short and sharp (0.05 mm in diameter at the tip). The needle became thick just above the point, so that no lateral bending of the needle could occur. This fact was verified under stroboscopic illumination. Thus a stiff platinum wire electrode with a diameter of 0.05 mm and a length of 1 mm could not be used because it showed definite bending for radial displacements.

It was desirable to have measurements of the sensitivity in the different directions made at the same time for both a constant static deformation and for vibrations. The following method was used for this purpose. The mechanical damping of the vibrating system was removed so that an applied direct current produced both a displacement and a series of transients having the natural frequency of the vibrating system. The vibrating system was placed on the basilar membrane near the round window, as shown by the heavy arrow in Fig. 14-36. A specially constructed switch made it possible to move the tip of the vibrating electrode in any of the three directions shown by the small arrows.

If the electrode was immersed in the perilymph toward the middle of the basilar membrane, the microphonics suddenly appeared at the moment the electrode touched the basilar membrane. At this moment the voltages were maximal for displacements in the radial direction, as shown by the arrow *r*. A direct current switched in and out produced the microphonics shown in oscillogram *a* of Fig. 14-37. Oscillogram *b* shows the microphonics produced by longitudinal displacements, and oscillogram *c* gives the microphonics for vertical movements of the membrane. Both trapezoidal displacements and 200-cps vibrations showed the same results: the microphonics were maximal for radial displacements of the tip of the electrode. Frequencies higher than 200 cps were seldom used because the directions of movement of the vibrating system were no longer clearly defined when the frequencies exceeded about 1000 cps.

If the tip of the electrode was moved deeper into the cochlear partition, the difference in sensitivity to vibration in different directions slowly diminished, in accordance with the situation shown in Fig. 14-32. But in general it was found that the more precisely the vibrations of the elec-

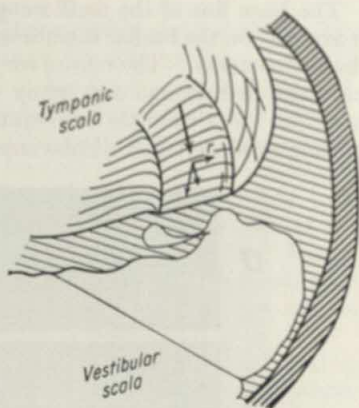


FIG. 14-36. The method of placement of the vibrating electrode on the basilar membrane near the round window. The arrows show radial, longitudinal, and vertical directions in which the electrode was vibrating.

trode were adjusted to follow the contours of the basilar membrane, the more pronounced the sensitivity in the radial direction became.

Near the helicotrema similar results were obtained. There it was necessary to insert the electrode deeper into the cochlear partition, because on the surface of Reissner's membrane the microphonics were not well defined.

The base line of the oscilloscope remained more stable when the electrode was on the basilar membrane near the stapes than when it was near the helicotrema. The reason for this is that the cochlear partition is soft near the helicotrema and many conditions can produce a change in its position. For example, involuntary contractions of the tensor-tympani muscle produce larger displacements near the helicotrema than near the

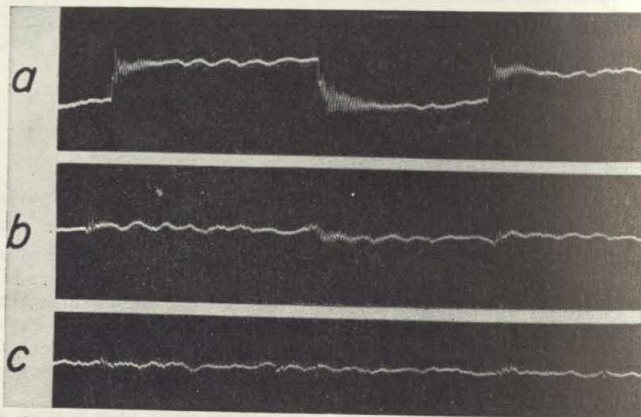


FIG. 14-37. Oscillograms of cochlear microphonics produced in the guinea pig by equal displacements of the electrodes in (a) radial, (b) longitudinal, and (c) vertical directions relative to the basilar membrane. The rapid waves are artifacts produced by movements of the table.

stapes. Therefore the tendons of both middle-ear muscles were severed in advance of all the measurements.

Electrodes with larger point diameters gave about the same results as those whose tips were 0.01 mm in diameter. The triangular utricular plate also showed a high degree of sensitivity to lateral displacements when measured with the three-directional vibrating electrode.

PLACE OF ORIGIN OF THE COCHLEAR MICROPHONICS*

The place of origin of the cochlear microphonics is difficult to determine. Location of the source of the microphonics is important, however, for if they do not originate close to the nerve endings of the eighth nerve they probably are not involved directly in the process of hearing.

When Wever and Bray (1) discovered the cochlear microphonics, it was assumed that these potentials were caused by the passage of nervous

* Article 65 as listed in the Author's Bibliography. Published in 1952.

activity through the eighth nerve. The properties of the microphonics pointed to the so-called telephone theory of hearing, and considerable importance was therefore attached to the role of the microphonics in hearing. Later Davis and Saul found that there is, in addition to the microphonics, a neural component in the eighth nerve. This apparent duplexity raises the question of the importance of the microphonics to hearing.

At one time or another practically all the movable parts of the cochlea have been suggested as the place of origin of the microphonics, with the exception of the basilar membrane, and it has been omitted because it consists of supporting tissues. Adrian (2) favored the endolymph and the perilymph; Hallpike and Rawdon-Smith (2) favored Reissner's membrane or the tectorial membrane; De Vries (3) favored the tectorial membrane; and Howe and Guild and also Davis, Derbyshire, Lurie, and Saul suggested the hair cells. Later Wever (3) too accepted the hair cells as the source of the microphonics and presented further details. But Davis, Gernandt, Riesco-MacClure, and Covell concluded that the microphonics have nothing to do with the actual process of hearing and are only a by-product.

This evolution looks rather discouraging, especially if we compare it, for instance, with the development of electrocardiography. In a short time electrocardiography became a very reliable tool. Perhaps one reason for this is that in electrocardiography most of the judgments were made from the time pattern of the potentials, and there was no need to localize the heart. But the time pattern of microphonics always corresponds to the sound pressure on the eardrum (as shown by Wever and Bray), and our whole interest is centered around the location of their source. Our conclusions about it are drawn chiefly from the amplitude differences at different places on the cochlea; yet this technique seems not to be reliable. If the place of origin is surrounded by insulating partitions, it is obvious that the distribution of the field can be strongly modified. Without a knowledge of the electrical properties of the partition we can draw no safe conclusion about the location of the electrical source.

In addition, there seems to be a certain difference between the electrical fields that we find in the common problems of physics and the electrical fields in living tissues. For example, in electronics a d-c battery can be represented, as shown in Fig. 14-38, as a tank with two open wires. The open wires must be insulated if a flow of current through the battery is to be avoided. But in a biological battery the positive and negative charges are completely balanced on the two sides of the cell partition, and even

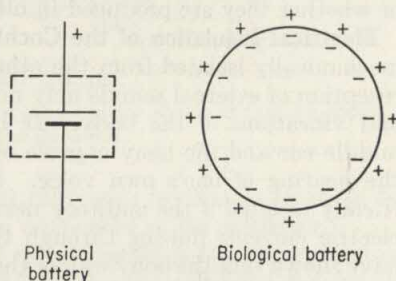


FIG. 14-38. Comparison of physical and biological batteries.

when the whole battery is immersed in a conducting fluid there is no flow of current and no loss of electric energy. A flow of current occurs only if the potential difference across the cell partition is no longer equal at all points on the partition. When this happens, almost all parts of the partition contribute to the current. The field of this integrative action is much more difficult to survey than the field produced by a practical point source such as a physical battery.

Consequently, without some knowledge of the electroanatomy (*i.e.*, the conductivity pattern) of the cochlea, it is difficult to draw conclusions about the distribution of electric currents in the tissues. The first approach to this problem was a measurement of the insulation of the various membranes and the electrical conductivity of the fluids. For these measurements a sharp search electrode was used to pierce through the cochlear partition with the aid of an automatic device, while at the same time the alternating and direct potentials were recorded automatically. With a sufficiently thin electrode this technique was found to produce little damage to the inner ear. The classical technique of cutting out parts of an organ and watching for the changes is too difficult to carry out here, and the effect on the tissues is too often traumatic. It is better to probe with a fine electrode and to look for the places where the electrical activity increases.

The next approach was an investigation of whether the most sensitive microphonics (first-order microphonics) are produced in the organ of Corti (the tectorial membrane plus the hair cells plus the cochlear nerves) or whether they are produced in other parts of the cochlea.

Electrical Insulation of the Cochlear Partition. The cochlea must be mechanically isolated from the other parts of the body in order that its reception of external sounds may not be disturbed by the internal sounds and vibrations of the body. It has previously been shown that the middle ear and the bony capsule of the cochlea are such as to suppress the hearing of one's own voice. Similarly, the cochlea must be electrically isolated if the auditory nerve fibers are not to be excited by the electric currents flowing through the body. Measurements (page 660) have shown that the bony wall of the cochlea insulates the hearing apparatus against the conductivity of the body fluids, *i.e.*, that the cochlea as a whole possesses electrical protection. But if the main process of hearing is located in the cochlear partition, then the basilar membrane and Reissner's membrane should show poor conductivity compared with the conductivity of the perilymph and endolymph. An examination of histological cross sections of the cochlea makes it easy to believe that the basilar membrane, with the superposed cells of Hensen, Claudius, and Corti, acts as an insulating layer. But it is difficult to understand how Reissner's membrane, which consists only of a single layer of cells, can serve the same purpose. An electric wire is most economically insulated when its insulation in the radial direction is exactly the same along its whole surface. If the electrical processes in the cochlear partition are really important, then we should expect the insulation of the endolymph from the perilymph to be the same all around the surface of contact of the

two fluids. That is to say, the insulation afforded by the basilar membrane should be of the same order of magnitude as the insulation afforded by Reissner's membrane.

The insulation of the two membranes was measured by introducing a potential difference across the cochlear partition between the vestibular and tympanic scalae by means of two electrodes connected to an oscillator. Then a third, indifferent electrode was introduced into one of the scalae, and a fourth microelectrode was placed close to the indifferent electrode. When the indifferent electrode and the microelectrode were close together, the potential difference between them was small. But as the microelectrode pierced through the cochlear partition the potential difference increased in discrete steps every time an insulating layer was

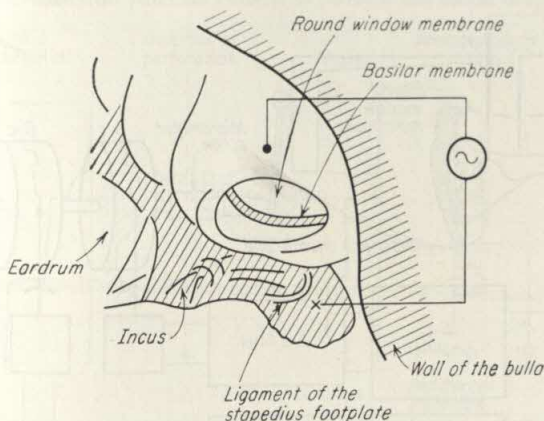


FIG. 14-39. View of the cochlea showing two places where electrodes may be placed to produce an electrical field across the cochlear partition.

perforated, until finally the potential difference became as large as the difference between the two electrodes connected to the oscillator.

A convenient place for this type of measurement is the round window. The bulla of a guinea pig was opened in such a way that the view of the middle ear under the microscope was similar to that shown in Fig. 14-39. The thin bony plate that covers one side of the stapedial footplate (to the right side of the figure) was removed. A small hole was then drilled in the vestibule close to the ligament at the right side of the stapedial footplate. This wall is usually thin, and there are no blood vessels nearby. One of the electrodes attached to the oscillator was cemented into the hole. The second electrode was fixed through a small hole near the rim of the round window in the tympanic scala, as shown in Fig. 14-39. These two electrodes produced a potential difference across the cochlear partition.

In order to introduce the two measuring electrodes into the scala above the basilar membrane, a small slit was made in the membrane of the round window. When the membrane of the round window is perforated, the

perilymph generally starts to stream out. With the deepening of the anesthesia this can be stopped or even reversed, with the result that air bubbles enter the tympanic scala. Considerable experience and careful observation were necessary before the pressure of the perilymph could be controlled so that no excess fluid flowed to the bottom of the bulla. With some guinea pigs it was not possible to control this pressure.

Figure 14-40 shows the general arrangement for registering the potential difference between the indifferent electrode and the perforating electrode. After the perforating electrode was appropriately placed, a motor was turned on that moved a micrometer screw slowly to the right. The micrometer screw in its turn caused a lever to move a microscope slide

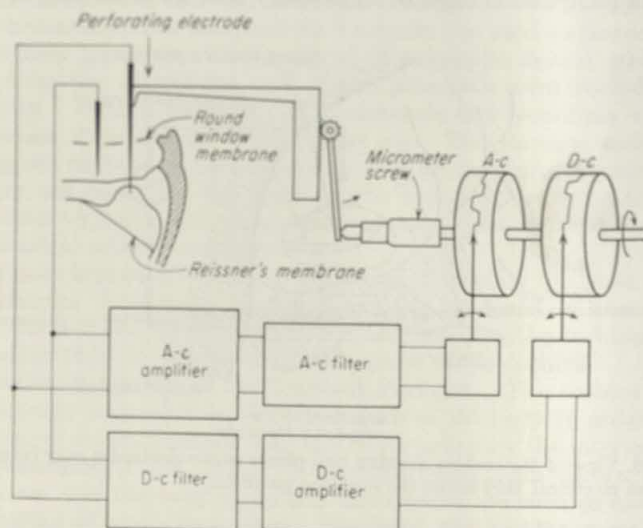


FIG. 14-40. Apparatus for automatic recording of potentials while an electrode was slowly pushed through the cochlear partition.

with a rack and pinion. The perforating electrode was attached to the microscope slide. On a shaft in common with the motor two recorders were attached, so that the alternating and direct potentials could be recorded simultaneously. The parallel displacement of the perforating electrode was calibrated and could be read in microns on the longitudinal shaft of the two recorders. For recording the finer details a dual-beam oscilloscope was connected to the amplifiers, and a photographic recorder was mounted on the same shaft as the other recorders.

The direct potentials were recorded to facilitate the location of the tip of the recording electrode. It had already been demonstrated (page 653) that the direct potential relative to the perilymph is negative inside the cell and positive in the endolymphatic space.

A representative set of measurements can be seen in Fig. 14-41. The curve on the extreme left shows the increase of the alternating potential

difference between the indifferent electrode in the tympanic scala and the perforating electrode as recorded during the progress of a perforation. When the electrode was moved down in the tympanic scala only a small potential difference was produced. This occurred because the current flow through the cochlear partition is not exactly perpendicular to the basilar membrane. The moment that the point of the electrode touched the mucus at the top of the basilar membrane, the a-c potential difference began to increase, and it jumped suddenly when the endolymphatic space was reached. While the electrode was traveling through the endolymphatic space, the increase of the potential was very small. Then a second sharp jump occurred when Reissner's membrane was perforated.

It is important to notice that the over-all increase of the potential across the basilar membrane plus its cells is of about the same magnitude as the

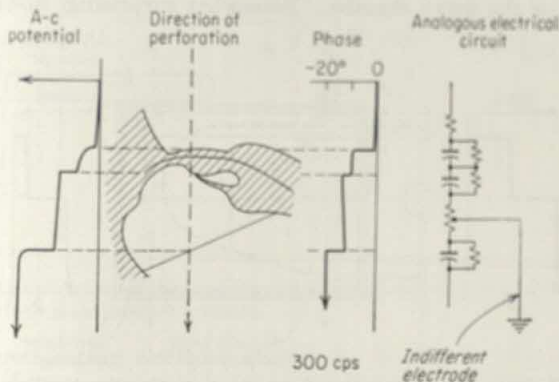


FIG. 14-41. Effects of perforating successive layers of the cochlear partition.

potential jump recorded from Reissner's membrane. Hence the insulation of the endolymph from the perilymph must be the same on both sides. Also the potential change across the perilymphatic space is relatively so small that both membranes must act as insulating layers.

During anoxia and at the onset of death the insulation afforded by the two membranes decreased, and the potential change produced as the electrode traveled through the endolymph became larger and larger compared with the jumps recorded at the membranes, which grew progressively smaller. Finally about 2 hr after death the jumps across the membranes became very small, and the voltage increased in a continuous fashion as the depth of the electrode was changed. In other words, the membranes then had about the same conductivity as the endolymph.

In addition to the magnitude of the a-c potential difference, it was possible also to measure the phase changes relative to the phase of the oscillator voltage. The right-hand side of Fig. 14-41 shows the phase shift of an a-c voltage of 300 cps during a perforation. Every time a membrane was perforated a negative phase shift occurred. As the electrode traveled through the endolymphatic space a small positive shift was produced. This indicates that the membranes have a capacity with

situation clear. A plastic basin with three compartments was filled with physiological salt solution. The two dividing walls of the basin, covered with filter paper saturated with the solution, formed a wall of low conductivity. The two electrodes leading to the oscillator were mounted on the left side of the basin. If an electrode was moved in the direction of arrows *a* and *b* as shown in the figure, the voltage jump produced at the basilar membrane was smaller on the right side than close to the oscillator. The reason for this is that along the flow lines in the tympanic scala there is a voltage drop from *a* to *b*, and this drop has to be subtracted from the voltage jump at the basilar membrane. To avoid this distortion the two electrodes from the oscillator need to be close to the modiolus and the measuring electrodes.

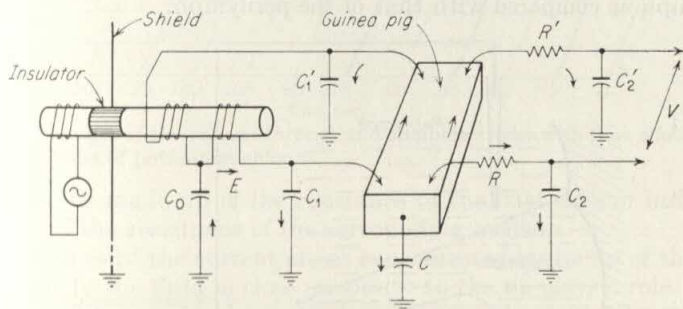


FIG. 14-43. An indication of the capacities between ground and parts of the measuring equipment which may produce artifacts.

2. The perforating electrode should be as thin as possible so that damage to the tissues may be held to a minimum. But this also increases the resistance of the electrode. And when the tips of the two measuring electrodes are brought as close together as possible, a large potential difference appears on the input terminals of the amplifier. This is so because every oscillator has a capacity to ground, and through this capacity and the electrodes a diffuse current may flow that produces a potential difference that is completely independent of the potential difference to be measured. This situation is represented in Fig. 14-43. On the left side of the figure is the output transformer of the oscillator, consisting of two symmetrical coils. The capacity to ground is C_0 . The figure also shows the scattered currents flowing through the capacity of wires C_1 and C_2 , the capacity of the experimental animal C , and the resistances R of the two measuring electrodes, all produced by the voltage E in one of the transformer coils. If all the electrical elements on the upper and lower sections of the drawing were exactly the same, the other coil would produce currents of the same magnitude but in the opposite direction. Unfortunately, this cannot be accomplished, and the result is a potential difference V between the input terminals of the amplifier, even if the tips of the electrodes are short-circuited. This disturbing effect was eliminated by reducing the capacity C_0 . The capacity of a sphere surrounded by a large box is for practical purposes the same as

the radius of the sphere. The two coils of the transformer had a diameter of 1.5 cm, and this made the capacity of the coils to ground about 4 cm. The transformer was an intermediate-frequency transformer of the type used in radios. The primary coil of the transformer was carefully shielded, so that the capacities of the oscillator did not play a role.

Electrical Conductivity of the Endolymph. In the previous section it was found that the whole organ of Corti and the endolymph are surrounded by an insulating layer. Since there is one connection between the endolymph and the tissues outside the cochlea, the potential of the endolymph is not floating. This is a perfect solution to the problem of isolating a sensitive organ from uncontrolled electric currents. But immediately it raises the question of the electrical conductivity of the endolymph as compared with that of the perilymph.

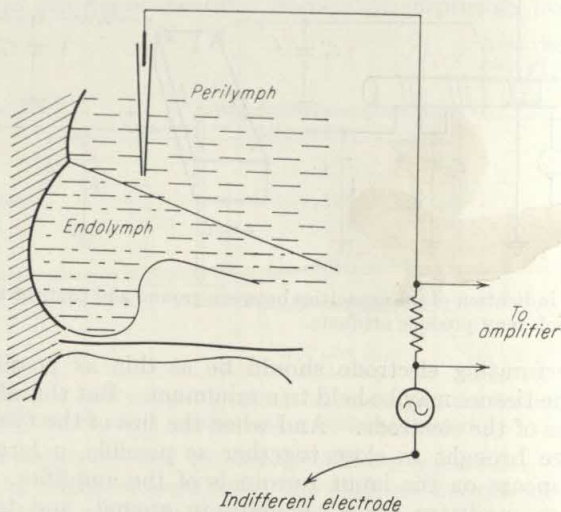


Fig. 14-44. Arrangement for the continuous measurement of electrode resistance.

It is obvious from Fig. 14-41 that the endolymph cannot be a highly insulating fluid, because the voltage drop produced as the electrode travels through the endolymph is very small. As a matter of fact, it is so small that it can hardly be used to measure the conductivity of the endolymph. The next method that was tried was to suck a small quantity of the endolymph into a thin capillary and to measure the conductivity there. But most of the measurements were made with a third method, one that was found more or less accidentally.

At the beginning of the measurements the tip of the automatically driven perforating electrode sometimes broke, and it was not possible to find out where or when it had happened. An automatic switch was devised that cut off the driving motor when the resistance of the electrode fell below a certain level. By recording the electrical resistance of the electrode continuously, it was possible to locate a break immediately by the drop in resistance. The circuit diagram for this device is shown

in Fig. 14-44. To control the automatic shutoff, a frequency of 7000 cps was used. This frequency was high enough not to disturb the other measurements. It was soon found that the resistance of the electrode changed not only when the electrode broke but also when the conductivity of the surrounding fluid changed, because the resistance of the

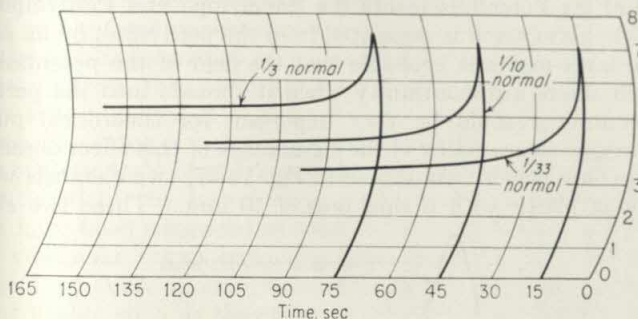


FIG. 14-45. Changes of the current through the microelectrodes with time when placed in dilute solutions of potassium chloride.

micropipette is made up of the resistance of the fluid column inside the capillary and the resistance of the surrounding medium.

The flow lines of the current are so concentrated at the tip of the electrode that only the fluid in close proximity to the tip plays a role. This made it possible to measure small quantities of the fluid. In order to increase the sensitivity, the capillary was filled with a fluid of good conductivity, such as a saturated solution of potassium chloride. The microelectrodes were stored in the same solution. If the electrodes were placed in a solution of lower conductivity, the current through the electrode decreased with time, as shown in Fig. 14-45. But after a short time a constant value was obtained, depending on the conductivity of the solution. It was possible to calibrate each electrode for a set of solutions, and these calibrations were reproducible.

Probably diffusion phenomena were responsible for the long period of adjustment of the resistance. But the outside fluid did not diffuse into the capillary to a great extent because if the electrode was placed in a saturated potassium chloride solution again, the current jumped almost to its original value as shown in Fig. 14-46, and only a slow further increase was caused by the diffusion into the capillary.

With the setup in Fig. 14-44 the conductivity of the perilymph was measured first. Reissner's membrane was then perforated, and the

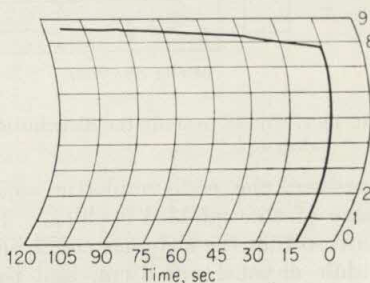


FIG. 14-46. Effect of replacing the pipette electrode after use in a solution of the same concentration as that inside it.

conductivity of the endolymph was observed. There was no significant difference between them. The conductivity of the endolymph at 37°C was found to be midway between the conductivity of a $\frac{1}{2} N$ and $\frac{1}{10} N$ potassium chloride solution at 18°C . This means that the conductivity of the endolymph is 2×10^{-2} mho per cm.

Spread of the Potentials inside the Endolymph and Perilymph. The fact that the endolymph is separated from the perilymph by an effective insulating layer makes it probable that the field of the potential in the endolymph shows a discontinuity when it spreads into the perilymph. This discontinuity could be very important for theoretical purposes. In order to gain some inkling of the significance of this effect observations were made on a model. As shown in Fig. 14-47, two channels were cut in a sheet of plastic with a thickness of 10 mm. These two channels

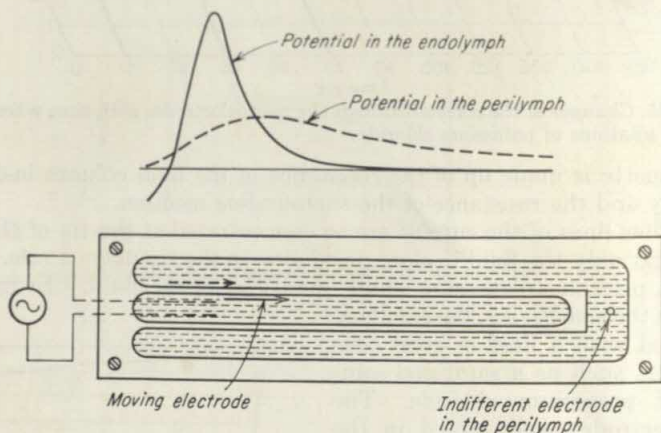


FIG. 14-47. Model to study the distribution of potentials arising from a small source in the "endolymph."

represent the endolymphatic space and the U-shaped perilymphatic space of the unfolded cochlea. The sheet was screwed onto a plastic plate so that the channels could be filled with water. The length of the middle channel was 6 cm, and the walls between the outer and inner channels had a thickness of 1 mm. These walls did not touch the bottom; a space of 1 mm was left open. This opening represented the conductivity between the endolymphatic and the perilymphatic spaces.

On the left side of the plastic model two platinum wire electrodes were placed in the middle channel so that the wires stood perpendicular to the bottom. These electrodes, representing a small a-c source in the cochlear partition, were connected to an oscillator. After these preparations had been made, a micropipette was moved 4 mm above the bottom along the inner and outer sides of one of the walls, and the potential relative to an indifferent electrode was recorded. The slopes of the two potentials along the wall are represented in the upper curves. For the measurements of the potentials in the perilymph the sensitivity of the amplifier was increased 15 db.

The movement of the electrode along the endolymphatic channel, represented by the full line, shows a definite peak close to the electrodes of the generator. But on the other side of the same wall this peak is flattened out and even displaced. This shows that any local disturbance inside the endolymph is spread out over practically the whole length of the cochlea in the perilymphatic space. Consequently, it is extremely difficult to base our conclusions about the local electrical disturbances inside the cochlear partition on measurements made outside the cochlear partition, unless these conclusions concern only temporary changes and the time involved is so short that no effect on the membranes surrounding the source of potentials can be expected.

Role of Reissner's Membrane in the Production of the Microphonics. As mentioned in the introduction, most of the movable parts of the cochlea have been suggested as sources of microphonics. Microphonics in the vestibular organ have also been described by Bleeker and de Vries and by Van Eyck. Practically every boundary between two different media, such as the surface between air and liquid, or between liquid and solid, produces microphonics if it is touched with a vibrating electrode (page 677). The voltages are usually small in inorganic systems, larger in organic, and largest in living tissues, where magnitudes of 10 to 30 μv are common. The vibrations of the perilymph, the endolymph, Reissner's membrane, the tectorial membrane, and the various cells of the organ of Corti all produce microphonics. But the aural microphonics are about five to ten times larger than the voltages found on ordinary organic boundaries. The question is, where are these larger microphonics produced? Perhaps these larger microphonics should be called microphonics of the first order to distinguish them from the smaller or second-order microphonics.

The movements of the perilymph do not produce first-order microphonics, because a vibrating electrode placed in the perilymph shows a sudden increase in voltage when the electrode touches the cochlear partition. This holds for the movements of the electrode in the direction of its longitudinal axis and for the lateral movements of the tip of the electrode. Therefore the first-order microphonics must be located in the cochlear partition or in the boundary of the partition.

In the investigation of the boundary surfaces, Reissner's membrane is of special interest. In order to decide whether the first-order microphonics are produced by Reissner's membrane or by the basilar membrane plus the organ of Corti the following experiment was performed. After the bony wall of the cochlea had been perforated, a small capillary was placed just above the cochlear partition. A small amount of the perilymph was sucked into the capillary, and this fluid column was set into vibration as shown in Fig. 14-48. One electrode was placed in the perilymph and the other in an indifferent location. If the pulsator was outside the cochlear partition, as shown in drawing *a* of Fig. 14-48, Reissner's membrane and the basilar membrane moved in phase, *i.e.*, downward if the fluid was pressed out of the capillary. But if Reissner's membrane was perforated and the tip of the pulsator was placed in the

endolymph, the outflow of the fluid from the capillary must move Reissner's membrane upward and the basilar membrane downward; *i.e.*, the two membranes must move in opposite phase as shown in drawing *b*. Consequently, the phase of the microphonics would reverse if Reissner's membrane were responsible for the production of the microphonics, and it would remain unchanged if the displacements of the basilar membrane and the cells of Corti were responsible for the microphonics.

The experiments showed that the amplitude of the microphonics increased when the tip of the pulsator was pushed down slowly. The moment Reissner's membrane was perforated the amplitude decreased a little, but the main voltage kept its phase. This fact indicates that some of the microphonics are produced by the movements of Reissner's membrane, but the main source lies on the basilar membrane. This

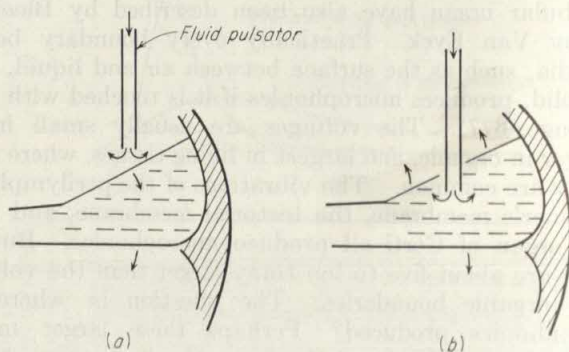


FIG. 14-48. Stimulation with a fluid pulsator above and below Reissner's membrane.

could be proved by pushing the tip of the pulsator through the basilar membrane, which immediately reversed the phase of the microphonics. This experiment was repeated at several points along the cochlear partition with the same results. This is a difficult experiment to perform on the tip of the cochlea, close to the helicotrema, because the distance between Reissner's membrane and the basilar membrane is very small. Near the round window the direction of the perforation can be changed by pushing through the basilar membrane first.

In a dying animal the first-order microphonics decreased in amplitude, until they became of the same order of magnitude as the second-order microphonics, and when this happened the potentials produced by Reissner's membrane were comparable with the potentials produced by the organs on the basilar membrane.

A schematic drawing of the pulsator is shown in Fig. 14-49. A plastic membrane was placed above a small hole and set in vibration with the help of an electromagnetic system. The resonant frequency of the plunger (about 300 cps) was the same as the driving frequency. A micropipette attached to a micromanipulator was connected to the hole, and a screw permitted the sucking of fluid through the pipette.

There is still another way of investigating the importance of Reissner's membrane in the production of the first-order microphonics. Close to the helicotrema, Reissner's membrane lies almost on the organ of Corti. It was possible to press Reissner's membrane down until it touched the organ of Corti without perforating the membrane or disturbing the cochlear partition. If a vibrating electrode was moved slowly downward, the potential suddenly rose as the electrode touched

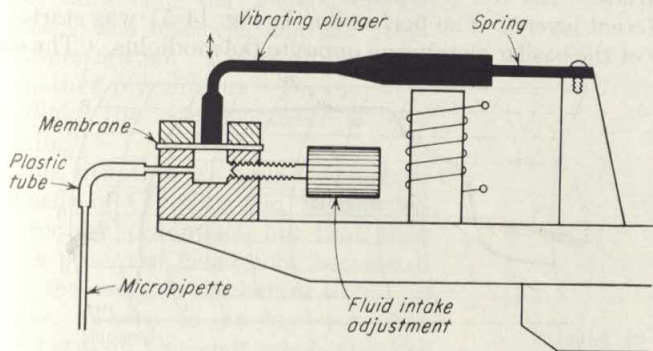


FIG. 14-49. Apparatus used to produce pulsations in the fluid of the micropipette.

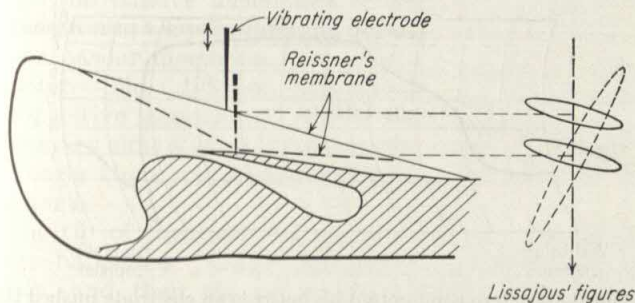


FIG. 14-50. Recording of potentials with the electrode in contact with Reissner's membrane, before and after touching the organ of Corti.

Reissner's membrane. During further downward movement the amplitude of the potentials did not change. But the moment the organ of Corti was reached the potential often reversed in phase and jumped to a high value, showing that the organ of Corti is more sensitive than Reissner's membrane. This situation is illustrated in Fig. 14-50 with the Lissajous figures seen on the oscilloscope.

Microphonics inside the Cochlear Partition. From the experiments with the pulsating fluid column it seems clear that we must look inside the cochlear partition for the place of origin of the first-order microphonics. If this conclusion is correct, we should expect to find larger microphonics in the endolymph than in the perilymph. Using the equipment described in Fig. 14-40, this hypothesis was tested by perforating the cochlear partition near the round window and recording automatically

the potential changes during the perforation of the different layers of the partition. At the beginning of the experiment the perforating and indifferent electrodes were close together just above the basilar membrane. The stimulating frequency was 300 cps. The potential changes during the movement of the electrode across the cochlear partition from the tympanic scala to the vestibular scala are shown in Fig. 14-51. The upper curve represents the a-c potentials and the lower curve the d-c potentials. The d-c potentials were convenient for identification of the different layers. The perforation in Fig. 14-51 was started on the outer side of the basilar membrane opposite the modiolus. The electrode

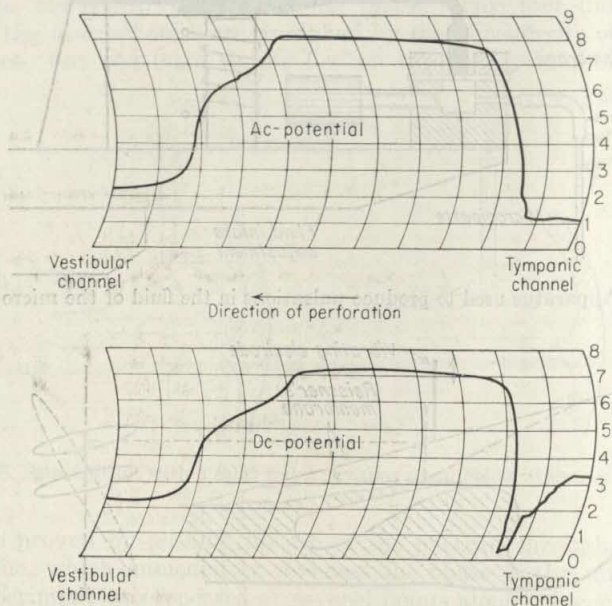


FIG. 14-51. Direct and alternating potentials between an electrode pushed through the cochlear partition and an indifferent electrode in the scala tympani.

made contact first with the loose cells lying on the basilar membrane. As the electrode penetrated further, the negative potential increased. After the fibrous layer of the basilar membrane was reached, the d-c potentials usually remained constant for a short time. Because of the toughness of this layer, the electrode displaced it for a moment until it was able to perforate it. The moment the electrode penetrated the cells of Claudius the potential jumped suddenly to a large negative value. A still further penetration brought the tip of the electrode into contact with the cells of Hensen, and the d-c potential decreased still further. Because the interior of these cells is negative relative to the perilymph, the cells resemble biological batteries (Fig. 14-38) with a negative charge inside the cell wall and a positive one outside the wall.

When the tip of the electrode penetrated to the endolymph, the d-c potentials suddenly jumped to a large positive value, and this value

remained constant all the while the electrode traveled through the endolymphatic space. The magnitude of the jump was of the order of 130 mv. At the same time the a-c potentials behaved differently. As seen in the upper curve of Fig. 14-51, the a-c potentials increased during the whole progress of the perforation. The increase proceeded in small steps at exactly the same time that a change in the d-c potentials was observed and the membrane was perforated. Figure 14-52 shows this on another preparation. On the original recordings the correspondence is even more striking.

From this situation we have to conclude that the cells of Claudius and Hensen are batteries for d-c potentials, but that they are not a-c potential generators, because if they were the a-c and d-c curves would be much alike. There is an a-c potential difference between the endolymph and the perilymph, and there is therefore a potential drop across the passive membranes of the cells of Hensen and Claudius and the fibrous layer of the basilar membrane, just as in a potentiometer. The different membranes have a capacitive component, and it was found that every time a small jump occurred in the a-c curve there was a small change in the phase angle.

When the tip of the electrode reached Reissner's membrane, one of two things happened. Either Reissner's membrane was perforated immediately, and then the a-c and d-c potentials in the perilymph dropped immediately to a low level, or the electrode failed to perforate Reissner's membrane. Figure 14-51 shows an instance in which Reissner's membrane was pushed ahead of the electrode. This produced a slow drop of the potentials until the perforation occurred, and then a faster drop took place. If Reissner's membrane was perforated in two steps, the d-c potential had a negative spike for a short time, indicating that Reissner's membrane presumably contains cells with negative contents. But as a whole, Reissner's membrane represents a passive membrane whose conductivity is not too different for alternating and direct currents. In general, the a-c potential showed a smaller drop than the d-c potential because of the capacity of the membrane.

Perforations close to the modiolus that passed through the hair cells and pushed upon the tectorial membrane from below were more complicated and will not be discussed here.

Summing up, we have the following picture. There are three types of tissues in the cochlear partition. (1) There are electrically indifferent

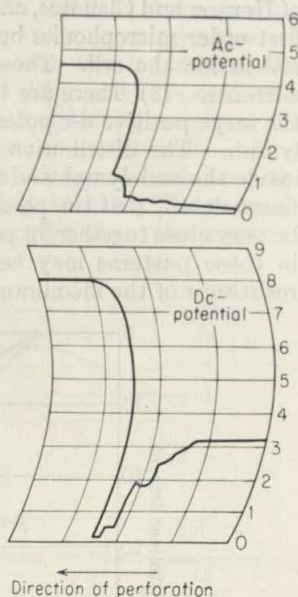


FIG. 14-52. Details of the perforation curves, showing that the Hensen and Claudius cells are d-c generators.

tissues, like the fibrous layer of the basilar membrane or the loose cells on the basilar membrane. They do not produce any potentials and act only as resistances. (2) There are cells with a wall, like the cells of Hensen and Claudius, and Reissner's membrane. They do not produce first-order microphonics but are like d-c batteries with a negative potential inside the cell. These cells are practically passive for alternating currents. (3) There are the highly active cells that are responsible for the large positive d-c potentials and the large a-c potentials in the endolymph. The distribution patterns of these large a-c and d-c potentials inside the endolymph and inside the perilymph are so similar, even to the finest detail, that the places of origin of the a-c and d-c potentials must be very close together, or perhaps even exactly the same. The differences in these patterns may be a consequence of the fact that the passive resistance of the membranes is dependent upon frequency.

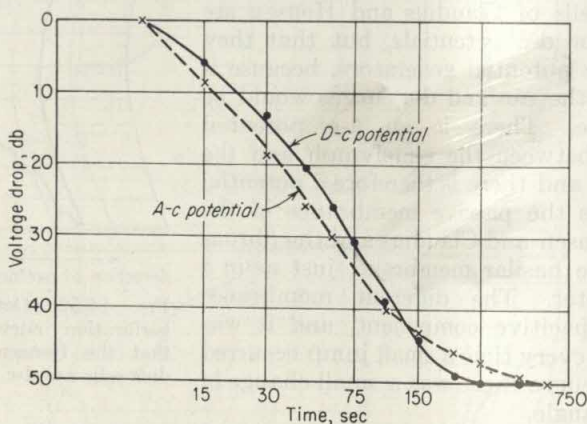


FIG. 14-53. Effects of anoxia on direct and alternating potentials when the recording electrode is in the endolymph.

This picture can be further supported by observations of conditions of anoxia and death. After administration of nitrogen the a-c and d-c potentials relative to an indifferent electrode showed a different course. During the first minute it was sometimes found that the d-c potentials increased in size and the a-c potentials showed a sharp decrease. They seemed to be independent of one another. But inside the cochlear partition the decays of the two potentials were more nearly alike, as shown in Fig. 14-53. Observations in the perilymph at the round window showed that the potentials are determined by at least two factors, the proper size of the generator voltage and the conductivity of the basilar membrane and Reissner's membrane. Both of these change under anoxia. The conductivity of the membranes was measured separately. The closer the approach to the place of origin of the microphonics was, the smoother the curves became. Figure 14-53 shows that the recording was closer to the sources of the first-order microphonics in the endolymph than any recording in the perilymph.

When the first-order microphonics dropped below $50 \mu\text{v}$, the field in the cochlea was changed by the second-order microphonics. There was typically a stage in which the a-c microphonics still showed an increase inside the endolymph, but at the same time the d-c potentials changed from a positive to a negative value. These negative potentials inside the cochlear partition were present as long as 2 hr after death; by then there was no longer an a-c potential difference between endolymph and perilymph. The source of these long-lasting negative d-c potentials is probably inside the cells of Hensen or Claudius. After death there is a deterioration of the insulation of the cell walls, and the endolymph therefore becomes negative (see Fig. 14-54). The negative potentials in the endolymph were always smaller than the negative potentials inside the cells of Claudius.

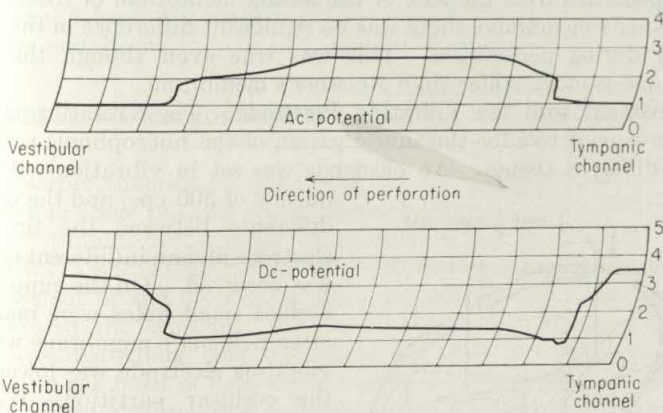


Fig. 14-54. Direct and alternating potentials in a dying animal, recorded from the endolymph.

In a fresh preparation the situation near the helicotrema was the same as near the round window. But it was more difficult to experiment near the helicotrema because the whole cochlear partition is much smaller there.

When the sound stimulation was increased, the size of the microphonics in the perilymph increased until a maximal output of about 1.8 mv was obtained near the round window for a sound of 300 cps.

Before these measurements were made, several control experiments were performed. The cochlear partition was brought into vibration by the sound waves acting on the eardrum. When the basilar membrane was touched with an electrode that was not vibrating, there was friction between the electrode and the basilar membrane, and the vibratory amplitude of the basilar membrane was decreased. To test the magnitude of this effect, a second electrode was introduced during the measurements of the a-c potentials in the endolymph. The change in the size of the a-c potentials was just perceptible, even when the second electrode was very close to the first one. The magnitude of the effect

depended on the diameter of the electrodes, which were always kept as small as possible, *i.e.*, just strong enough to perforate the fibrous layer of the basilar membrane.

A second way to test the friction between the electrode and the basilar membrane was to reverse the motor used to drive the electrode after the perforation had been made. The electrode was then pulled out, and an exact mirror image of the recorded curve was obtained with thin electrodes, giving the same jumps of the potential at the same spatial distances. If the electrode was too large, the membranes adhered to it and a displacement appeared between the two records. This test was always made because it constituted the most convenient method for determining the optimal size for the electrode.

A third test indicated that, regardless of whether the cochlear partition was approached from the side of the basilar membrane or from the side of Reissner's membrane, there was no significant difference in the voltage pattern during perforation. This was true even though the basilar membrane is much stiffer than Reissner's membrane.

Experiment with the Vibrating Electrode. The vibrating electrode is a convenient tool for the investigation of the microphonic sensitivity of the different tissues. An electrode was set in vibration with a frequency of 300 cps, and the potential difference between the tip of the electrode and an indifferent electrode was observed. On the cupola of the cochlea small holes were made, and after Reissner's membrane was slit a vibrating electrode was lowered into the cochlear partition. With the amplitude of the vibrating electrode kept constant it was found that the amplitude of the microphonics was greatest when the outer rim of the tectorial membrane was touched.

This maximum was not sharp, but microphonics produced by the cells of Hensen and Claudius were usually smaller than those recorded on the outer border of the tectorial membrane. The reason for this may be that, because the tectorial membrane is much stiffer than the cells of

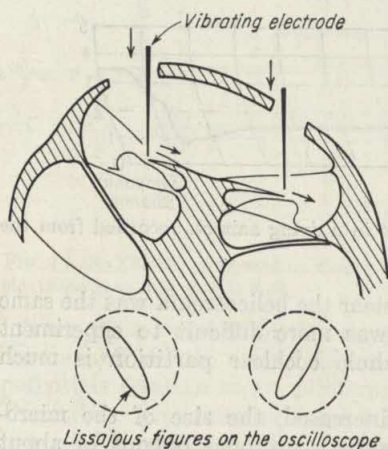


FIG. 14-55. The phase of the microphonics as related to the orientation of the vibrating electrode relative to the organ of Corti.

Hensen and Claudius, touching the tectorial membrane produces a vibration on a larger area. This usually increased the amplitudes of the microphonics.

When the axis of the modiolus was in a vertical position and the vibrating electrodes were placed parallel to it on opposite sides of the cochlea at points of exact anatomical correspondence, the phase of the microphonics was usually reversed, as indicated by the Lissajous figures

in Fig. 14-55. This can be explained if we assume that the organ of Corti is sensitive to displacements in the radial direction. As can be seen from the figure, the cochlear partition is wound in a spiral around the modiolus, and the plane of the cochlear partition is inclined relative to the axis of the modiolus. On one side of the modiolus a downward movement of the electrode produces a radial movement toward the modiolus; and on the other side it produces a movement away from the modiolus. This would explain the phase reversal. Correct performance of this experiment requires an elaborate apparatus, because displacements of the organ of Corti that are too large (unphysiological) can alter the phase of the microphonics to a greater extent than the amplitude.

These experiments seem to indicate that the organ of Corti plays an important role in the production of the first-order microphonics. Furthermore, it was found that the organ of Corti is electrically isolated and protected from the perilymph by both Reissner's membrane and the basilar membrane.

SHEARING MICROPHONICS PRODUCED BY VIBRATIONS IN THE COCHLEA*

In the earlier theories of hearing the up-and-down movements of the hair cells and their pushing on the tectorial membrane were considered to be the stimulus for hearing. A system of stimulation different in principle was assumed for the otoliths. J. Breuer suggested that it was not the weight of the otoliths on the hair cells but the shearing forces that produced the stimulus. This heterogeneity of organs so closely related was disturbing from the point of view of evolution. Later Kuile, on the basis of histological evidence, developed a well-founded theory in which the shearing between the reticular membrane and the tectorial membrane was considered to be the stimulus.

Within the last few years this whole problem received a new impetus when Holst in unusually precise experiments showed that in fish it is only the shearing forces of the otoliths that determine the position of the fish and not their positive or negative pressure effects. If we look for a mechanical system in the organ of Corti able to transform the relatively small streaming forces of the movements of the perilymph into larger forces for the elastic tissues of the organ of Corti, we find that a matching of mechanical impedances of this kind exists only for the shearing forces between the tectorial membrane, the reticular membrane, and the basilar membrane. Matching of this kind seems to be important if we consider the high sensitivity of the ear, and, as measurements show, the middle ear with the ossicles and the eardrum represents a perfect matching device between the very light air and the large masses of fluid set in vibration in the cochlea by a sound.

Holst pointed out that shearing forces have an advantage over pressure as a stimulus because they have two degrees of freedom in the two perpendicular directions, whereas pressure acts only in one direction. As

* Article 68 as listed in the Author's Bibliography. Published in 1953.

already mentioned (page 497), vibrations in the organ of Corti are largely radial on one side of the point of maximal stimulation and largely longitudinal on the other side.

To find out what types of force produce the microphonics in the cochlea a small section of the tissue was stimulated with a vibrating needle. In

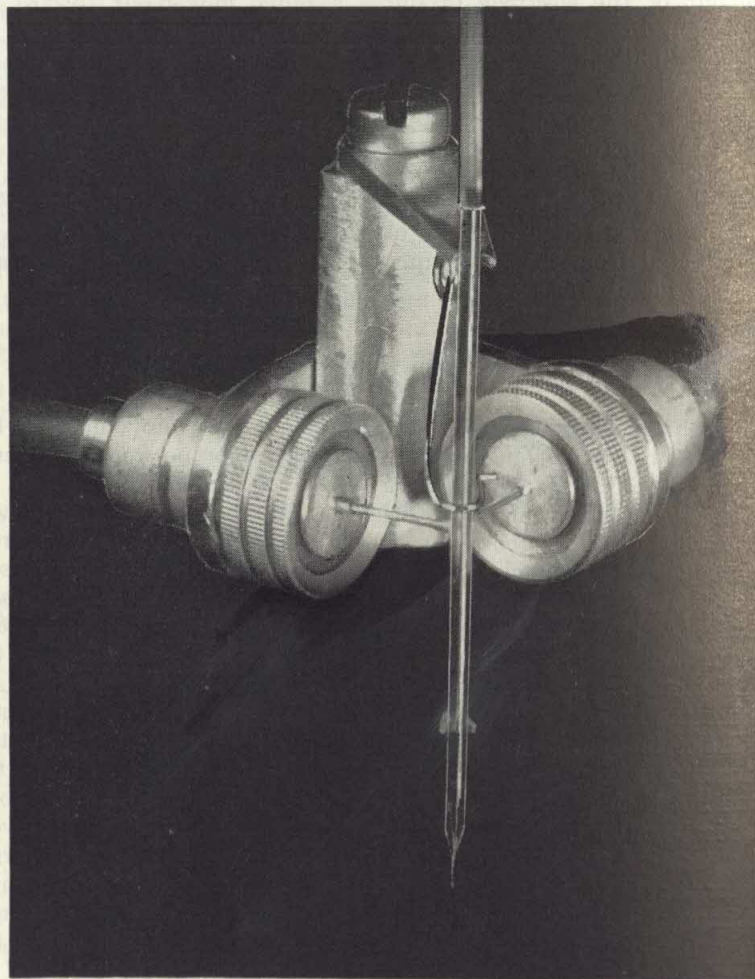


Fig. 14-56. Apparatus for producing lateral vibrations of a needle in any desired direction perpendicular to the axis of the needle.

one case the movement of the needle along its axis was up and down, in the other case from side to side. The equipment used in producing the lateral movements is shown in Fig. 14-56.

To avoid an electrical field near the preparation, the needle was separated from the sound source (two loudspeakers) by a 2-ft tube. To each loudspeaker a membrane was attached through a tube and set

into vibration by the sound. The two membranes with a piston glued to them permitted the needle to move along the two horizontal axes. By means of a special switch it was possible to adjust the relative intensity of the two sounds in such a way that the needle vibrated in any desired lateral direction with about the same amplitude. It sometimes happened that there was a small phase difference between the two movements of the pistons, and the tip of the needle described an ellipse rather than a line. This was corrected by slightly compressing one of the plastic tubes coming from the loudspeakers.

Unfortunately it is difficult to produce either small local pressures or shearing forces in a pure form. As shown in Fig. 14-57, they always occur together. A downward movement of the needle tip is accompanied by a suction on both sides constituting shearing forces, and a lateral displacement of the needle tip on the surface of an elastic material pushes the material before it and pulls it behind. But if the elastic material is covered with a stiff layer, as in the organ of Corti, the difference between the pressure and the shearing force becomes more specific. Therefore a blunt needle tip pressed lightly on the tectorial membrane or on the reticular membrane produces mostly shearing forces if the tip vibrates laterally. But a perpendicular displacement of the plate on the surface of the softer tissues always produces a lateral flow of the tissue. Perhaps this is the reason that vibrating electrodes or needles give more reproducible results when moved parallel to the surface than when moved perpendicularly to the surface.

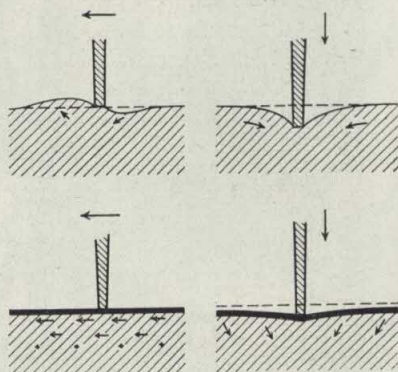


FIG. 14-57. The production of pressures and shearing forces in an elastic material: (a) shows a perpendicular and (b) a lateral displacement for a uniform material; (c) shows a perpendicular and (d) a lateral displacement for a material covered with a stiff layer. The arrows within the material represent its movements.

The fact that the direction of the vibrations of the reticular membrane during exposure to a tone changes from radial to longitudinal along the basilar membrane near the point of maximal amplitude leads us to expect that the microphonics produced in the two directions may be different. Therefore the organ of Corti was touched with a laterally vibrating needle at different points, and the direction of the lateral movement was rotated around the axis of the needle. At the same time one electrode was placed in the perilymph or endolymph near the vibrating needle and another electrode in the muscles of the neck, and the microphonics were observed. Several disturbing effects were present during these observations.

The vibrating needle produced electrocapillary potentials at the peri-

lymph-air boundary (*cf.* page 677). These potentials decreased with the diameter of the needle at the surface. It was found desirable to keep the level of the fluid above the organ of Corti low, so that a thin needle with concave sides did not bend when the tissue was touched. Otherwise the vibrations were larger at the stem of the needle than at the tip, and then the electrocapillary potentials became larger relative to the microphonics. The size of the microphonics relative to the electrocapillary potentials was always greater than 10:1. After the needles were used

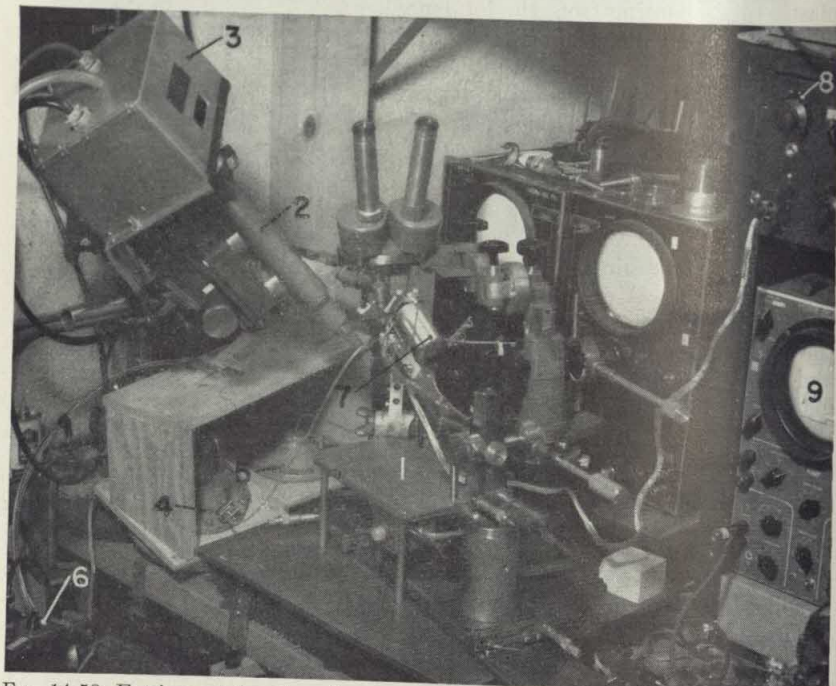


FIG. 14-58. Equipment for observing the microphonics produced by shearing movements of the organ of Corti. 1, operating table; 2, slit lamp; 3, stroboscope; 4, loudspeaker with plastic tube; 5, a second loudspeaker; 6, adjusting mechanism for the vibrating needle; 7, preamplifier; 8, amplifier; 9, oscilloscope.

for some time they were replaced, because the slightest dirt on the needle increased the electrocapillary potentials.

Another difficulty was that the vibrations of the tip of the needle were spread out in the tissues. At high frequencies there were traveling waves with regions of opposite phase, which was highly disturbing. At 150 cps all the deformations as seen through the stroboscope were purely elastic and in the same phase. The fact that touching the organ of Corti on one spot produced larger microphonics than on another spot does not necessarily mean that one place was more sensitive than the other, because in one case the covering layer on the sensitive cells could be stiffer, so that a larger number of cells were stimulated. This pro-

duced larger microphonics probably because connection of several generators in parallel decreases their resistance and makes the voltage across the perilymph larger. In comparing sensitivity for lateral movements in different directions, great care was taken to adjust the area of the vibrations to the same size by changing the lateral amplitudes of the vibrations or the depth to which the needle was pressed into the surface. The impression of the needle in the tectorial membrane or the reticular membrane had to be carried out automatically, very slowly, and under continuous stroboscopic control.

The whole equipment is shown in Fig. 14-58. At the left is the mercury arc for stroboscopic illumination, and in the wooden box are the two loudspeakers with the plastic tube, one provided with a clamp for fine adjustments of phase. The vibrating needle and the preamplifier are situated under the stereoscopic microscope and attached to the automatic driving system for slow downward movement.

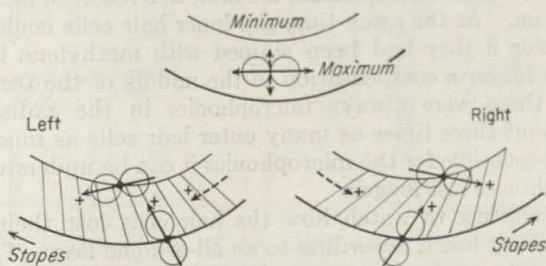


FIG. 14-59. Directional sensitivity of the microphonics for a laterally vibrating needle placed on the outer, middle, and inner edges of the tectorial membrane.

For all observations, the perilymph above Reissner's membrane was removed by suction, and Reissner's membrane was peeled off. When the laterally vibrating needle tip was placed on the outer edge of the slightly stained tectorial membrane, it was found that the sensitivity of the microphonics was maximal in the direction of the fibers of the tectorial membrane and minimal (zero) in a direction perpendicular to the fibers of the reticular membrane. This situation is shown in Fig. 14-59 for the left and right cochleae of a guinea pig as seen from the ventral side.

If the amplitude of the lateral vibrations was kept constant and at the same time the direction of the vibrations was reversed, the amplitude of the microphonics showed a continuous change in size. The relative size of the microphonics can be found for any direction by running a line through the point in Fig. 14-59 where the two circles touch. The length of the line enclosed by the circle represents the relative size of the microphonics for the different directions. The measurements of the microphonics in the different directions did not give precise circles, probably because of the interaction between the two systems, but they were acceptable as first approximations. The directional characteristic of the microphonics is therefore similar to the directional characteristic of a velocity microphone.

At the inner edge of the tectorial membrane close to the modiolus the angle of maximal sensitivity is changed and is more in the direction where the minimum was before. The direction of sensitivity on the inner edge lies between the tangent of the edge and a direction perpendicular to the fibers of the tectorial membrane. It was not possible to observe this direction precisely because there was interaction with the microphonics on the outer edge. In a fresh preparation, the maximal size of the two microphonics on inner and outer edges was about the same, and if the tip of the needle was placed somewhere between the inner and outer edges, it was possible to find a place where the direction of maximal sensitivity was along the longitudinal axis of the organ of Corti and the minimum was clearly in the radial direction. This seems to indicate that somewhere in the middle of the tectorial membrane the microphonics from the two edges add together and compensate each other in the radial direction.

In general the inner microphonics die first, as a result of lack of oxygen, cold, and so on. At the same time the inner hair cells could be seen to lose their color if they had been stained with methylene blue. Then there was no longer a compensation in the middle of the tectorial membrane, and there were always microphonics in the radial direction. There are about three times as many outer hair cells as inner hair cells. If they are responsible for the microphonics it can be understood why the outer microphonics last longer.

It was interesting to watch how the hair cells lost their methylene blue color. They lost it according to an all-or-none law. There was no slow simultaneous fading away of the color in all the cells. Rather, some cells suddenly turned white while others kept their color as before. At the end only a few blue cells were left in the whole organ of Corti, but they often remained so for a whole day.

The fact that the microphonics recorded at the inner edge can disappear without any changes taking place in those at the outer edge provides an opportunity of testing whether the microphonics are produced by the forces acting on the tissue or through a deformation of the tissue. If a needle was inserted into the inner edge of the tectorial membrane and pushed radially outward, the sensitive part of the organ of Corti was displaced, as seen in Fig. 14-60. If the force on the tissue is important as a stimulus, then placing the needle on the outer edge and moving it outward in the same way should give microphonics of reversed polarity. This is true because now the sensitive part of the organ of Corti is pulled rather than pushed. On the other hand, if deformation constitutes the stimulus, no difference should appear. When this experiment was tried there was no change, and therefore the shearing deformation is the stimulus.

The mercury-arc lamp with its pulses of 2000 volts was shielded so well that it did not disturb the microphonics. It was therefore possible to observe the movements of the tip of the needle and at the same time to observe on a cathode-ray oscilloscope the size of the microphonics. They reached their maximum growth every time the needle was in an extreme

position. To show the polarity of the microphonics the arrow in Fig. 14-59 points to the place at which the electrode is positive relative to an indifferent electrode. The active electrode was placed on top of the completely intact Reissner's membrane, and the indifferent electrode was placed in the neck of the guinea pig. At the same time the whole cochlea had to be completely filled with perilymph as in the normal situation. The dashed arrow parallel to the longitudinal axis of the organ of Corti indicates the direction of displacement of the needle placed in the middle of the tectorial membrane, which made the electrode in the perilymph positive relative to the electrode in the neck.

It happened several times that the polarity was the reverse of the situation represented in Fig. 14-59. The reason for this can be seen in Fig. 14-61. The microphonics are probably produced by a generator

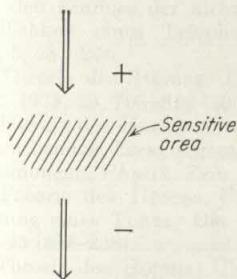


FIG. 14-60. The sensitive region of the organ of Corti is represented by cross-hatching. The arrows *a* and *b* indicate the opposed directions of pressure when the tectorial membrane is pushed on its outer and inner edges.

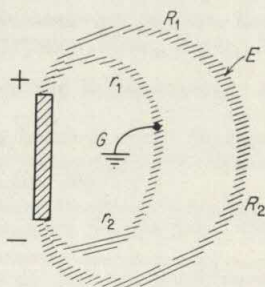


FIG. 14-61. Sketch showing how the potential difference between an indifferent electrode *G* and an active electrode *E* may be reversed in polarity if the shunt resistances in the field are altered. The rectangle represents the potential generator.

between the tectorial membrane and the basilar membrane. This generator is shunted by the endolymph and perilymph represented in Fig. 14-61 by the resistance $r_1 + r_2$. The connection to the indifferent electrode in the neck may lie between r_1 and r_2 . A similar shunt with a similar electrical tap is produced by the perilymph and the electrode *E*. It seems probable that r_1/r_2 is larger than R_1/R_2 , because if R_1 was increased by sucking away the perilymph above Reissner's membrane, the microphonics in the cases observed reversed their polarity, compared with the situation in which the whole channel of the cochlea was filled with perilymph. The polarity of the microphonics was always determined with Reissner's membrane unperforated, so that the conductivities were normal. The integrity of Reissner's membrane was tested with the microscope after staining with methylene blue, at a time when all the nuclei could be seen clearly.

If the perilymph was sucked off and Reissner's membrane and the tectorial membrane were peeled back, the microphonics were still obtained on placing the tip of the needle on the reticular membrane. But the

change of sensitivity in the lateral direction was no longer well developed. If the whole organ of Corti was taken away with a fine painter's brush the microphonics disappeared, and only by increasing the amplitude of the lateral vibrations, especially in the longitudinal direction, was it possible to extend the vibrations along the basilar membrane far enough that new, undestroyed cells could be reached.

These results lead to the conclusion that the tectorial membrane with its attachment to the reticular membrane is mainly responsible for the difference in directional sensitivity between the inner and outer edges of the organ of Corti.



The diagram illustrates the mechanical coupling between the tectorial membrane and the organ of Corti. The tectorial membrane is shown as a hatched area, and the organ of Corti is represented by vertical bars. Arrows indicate the direction of vibration: vertical arrows for longitudinal vibration and horizontal arrows for lateral vibration. The diagram shows that the tectorial membrane is attached to the reticular membrane, which is the base of the organ of Corti. This attachment is responsible for the difference in directional sensitivity between the inner and outer edges of the organ of Corti.

between the tectorial membrane and the basilar membrane. The organ of Corti is shown as a series of vertical bars, and the tectorial membrane is shown as a hatched area. Arrows indicate the direction of vibration: vertical arrows for longitudinal vibration and horizontal arrows for lateral vibration. The diagram shows that the tectorial membrane is attached to the reticular membrane, which is the base of the organ of Corti. This attachment is responsible for the difference in directional sensitivity between the inner and outer edges of the organ of Corti.

The diagram illustrates the mechanical coupling between the tectorial membrane and the organ of Corti. The tectorial membrane is shown as a hatched area, and the organ of Corti is represented by vertical bars. Arrows indicate the direction of vibration: vertical arrows for longitudinal vibration and horizontal arrows for lateral vibration. The diagram shows that the tectorial membrane is attached to the reticular membrane, which is the base of the organ of Corti. This attachment is responsible for the difference in directional sensitivity between the inner and outer edges of the organ of Corti.

AUTHOR'S BIBLIOGRAPHY

The numbers in brackets at the end of a reference indicate the pages of this book where the article is to be found. If there are no numbers in brackets, the article is not included in this book.

1. Über den Einfluss der nichtlinearen Eisenverzerrungen auf die Güte und Verständlichkeit eines Telephonie-Übertragungssystems, *Elektr. Nachr. Techn.*, 1928, 5, 231-246.
2. Zur Theorie des Hörens; Die Schwingungsform der Basilarmembran, *Physik. Zeits.*, 1928, 29, 793-810 [404-429].
3. Zur Theorie des Hörens; Über die Bestimmung des einem reinen Tonempfinden entsprechenden Erregungsgebietes der Basilarmembran vermittelt Ermüdungserscheinungen, *Physik. Zeits.*, 1929, 30, 115-125 [354-368].
4. Zur Theorie des Hörens; Über die eben merkbare Amplituden- und Frequenzänderung eines Tones; Die Theorie der Schwebungen, *Physik. Zeits.*, 1929, 30, 721-745 [207-238].
5. Zur Theorie des Hörens; Über das Richtungshören bei einer Zeitdifferenz oder Lautstärkenungleichheit der beiderseitigen Schalleinwirkungen, *Physik. Zeits.*, 1930, 31, 824-835, 857-868 [272-301].
6. Über das Fechnersche Gesetz und seine Bedeutung für die Theorie der akustische Beobachtungsfehler und die Theorie des Hörens, *Ann. Physik*, 1930, 7, 329-359.
7. Sur la théorie de l'audition, *L'ann. psychol.*, 1930, 31, 63-96 [238-257].
8. Über die Messung der Schwingungsamplitude fester Körper, *Ann. Physik*, 1931, 11, 227-232 [51-53].
9. Bemerkungen zur Theorie der günstigsten Nachhalldauer von Räumen, *Ann. Physik*, 1931, 8, 851-873 [369-383].
10. Über die Ausbreitung der Schallwellen in anisotropen dünnen Platten, *Zeits. Physik*, 1932, 79, 668-671.
11. Zur Theorie des Hörens bei der Schallaufnahme durch Knochenleitung, *Ann. Physik*, 1932, 13, 111-136 [128-147].
12. Über den Einfluss der durch den Kopf und den Gehörgang bewirkten Schallfeldverzerrungen auf die Hörschwelle, *Ann. Physik*, 1932, 14, 51-56 [267-271].
13. Über die Schallfeldverzerrungen in der Nähe von absorbierenden Flächen und ihre Bedeutung für die Raumakustik, *Zeits. tech. Physik*, 1933, 14, 6-10 [392-399].
14. Über die Hörsamkeit der Ein- und Ausschwingvorgänge mit Berücksichtigung der Raumakustik, *Ann. Physik*, 1933, 16, 844-860 [58-60, 321-332].
15. Über den Knall und die Theorie des Hörens, *Physik. Zeits.*, 1933, 34, 577-582 [314-321].
16. Über die Hörsamkeit kleiner Musikräume, *Ann. Physik*, 1934, 19, 665-679 [383-392].
17. Über die nichtlinearen Verzerrungen des Ohres, *Ann. Physik*, 1934, 20, 809-827 [332-344].
18. Über die Hörsamkeit von Konzert- und Rundfunksälen, *Elektr. Nachr. Techn.*, 1934, 11, 369-375.
19. Physikalische Probleme der Hörphysiologie, *Elektr. Nachr. Techn.*, 1935, 12, 71-83.

20. Über akustische Reizung des Vestibularapparates, *Pflüg. Arch. ges. Physiol.*, 1935, 236, 59-76.
21. Über akustische Rauigkeit, *Zeits. tech. Physik*, 1935, 16, 276-282 [344-354].
22. Über die Herstellung und Messung langsamer sinusförmiger Luftdruckschwankungen, *Ann. Physik*, 1936, 25, 413-432 [60-72].
23. Über die Hörschwelle und Fühlgrenze langsamer sinusförmiger Luftdruckschwankungen, *Ann. Physik*, 1936, 26, 554-566 [257-267].
24. Fortschritte der Hörphysiologie, *Zeits. tech. Physik*, 1936, 17, 522-528.
25. Zur Physik des Mittelohres und über das Hören bei fehlerhaftem Trommelfell, *Akust. Zeits.*, 1936, 1, 13-23 [104-115].
26. Photoelektrische Fourieranalyse eines Kurvenzuges, *Elektr. Nachr. Techn.*, 1937, 14, 157-161.
27. Über subjektive harmonische Teiltöne, *Akust. Zeits.*, 1937, 2, 149.
28. Über die mechanische Frequenzanalyse einmaliger Schwingungsvorgänge und die Bestimmung der Frequenzabhängigkeit von Übertragungssystemen und Impedanzen mittels Ausgleichsvorgängen, *Akust. Zeits.*, 1937, 2, 217-224 [78-81].
29. Über die Entstehung der Entfernungsempfindung beim Hören, *Akust. Zeits.*, 1938, 3, 21-31 [301-313].
30. Psychologie und Fernsprechtechnik, *Forsch. u. Fortsch.*, 1938, 14, 342-344.
31. Über die piezoelektrische Messung der absoluten Hörschwelle bei Knochenleitung, *Akust. Zeits.*, 1939, 4, 113-125 [148-163].
32. Über die mechanisch-akustischen Vorgänge beim Hören, *Acta Oto-laryngol.*, 1939, 27, 281-296, 388-396 [31-32].
33. Über die Vibrationsempfindung, *Akust. Zeits.*, 1939, 4, 316-334.
34. Über die Empfindlichkeit des stehenden und sitzenden Menschen gegen sinusförmige Erschütterungen, *Akust. Zeits.*, 1939, 4, 360-369.
35. Über die Stärke der Vibrationsempfindung und ihre objektive Messung, *Akust. Zeits.*, 1940, 5, 113-124.
36. Über die Sicherheit und Reproduzierbarkeit künstlerischer Urteile beim Rundfunk, *Arbeitsstagung der deutschen Fachbeiräte für Sing- und Sprechkultur in Wien*, April, 1940.
37. The neural terminations responding to stimulation of pressure and vibration, *J. Exper. Psychol.*, 1940, 26, 514-519.
38. Über die Messung der Schwingungsamplitude der Gehörknöchelchen mittels einer kapazitiven Sonde, *Akust. Zeits.*, 1941, 6, 1-16 [20-23, 30-31, 53-57, 95-104].
39. Über die Elastizität der Schneckentrennwand des Ohres, *Akust. Zeits.*, 1941, 6, 265-278; On the elasticity of the cochlear partition, *J. Acoust. Soc. Amer.*, 1948, 20, 227-241 [23-25, 469-480].
40. Über die Schallausbreitung bei Knochenleitung, *Zeits. f. Hals-, Nasen-, Ohrenheilk.*, 1941, 47, 430-442.
41. Über das Hören der eigenen Stimme, *Anz. Akad. Wiss., Wien, Math.-nat. Kl.*, 1941, 9, 67.
42. Über die Schwingungen der Schneckentrennwand beim Präparat und Ohrenmodell, *Akust. Zeits.*, 1942, 7, 173-186; The vibration of the cochlear partition in anatomical preparations and in models of the inner ear, *J. Acoust. Soc. Amer.*, 1949, 21, 233-245 [30, 429-446].
43. Über die Resonanzkurve und die Abklingzeit der verschiedenen Stellen der Schneckentrennwand, *Akust. Zeits.*, 1943, 8, 66-76; On the resonance curve and the decay period at various points on the cochlear partition, *J. Acoust. Soc. Amer.*, 1949, 21, 245-254 [446-460].
44. Über die direkte mikroskopische Ausmessung der Resonanzschärfe und Dämpfung der sogenannte Ohrenresonatoren, *Forsch. u. Fortsch.*, 1943, 19, 364-365.
45. Über die mechanische Frequenzanalyse in der Schnecke verschiedener Tiere, *Akust. Zeits.*, 1944, 9, 3-11 [500-510].
46. Über die Frequenzauflösung in der menschlichen Schnecke, *Acta Oto-laryngol.*, 1944, 32, 60-84 [535-539].
47. The variation of phase along the basilar membrane with sinusoidal vibrations, *J. Acoust. Soc. Amer.*, 1947, 19, 452-460 [38-40, 460-469].

48. The sound pressure difference between the round and the oval windows and the artificial window of labyrinthine fenestration, *Acta Oto-laryngol.*, 1947, 35, 301-315 [115-126].
49. A new audiometer, *Acta Oto-laryngol.*, 1947, 35, 411-422 [81-91].
50. The recruitment phenomenon and difference limen in hearing and vibration sense, *Laryngoscope*, 1947, 57, 765.
51. (With W. A. Rosenblith), The early history of hearing: Observations and theories, *J. Acoust. Soc. Amer.*, 1948, 20, 727-748.
52. Vibration of the head in a sound field, and its role in hearing by bone conduction, *J. Acoust. Soc. Amer.*, 1948, 20, 749-760 [163-181].
53. The structure of the middle ear and the hearing of one's own voice by bone conduction, *J. Acoust. Soc. Amer.*, 1949, 21, 217-232 [181-203].
54. Über die Mondillusion, *Experientia*, 1949, 5, 326.
55. The moon illusion and similar auditory phenomena, *Amer. J. Psychol.*, 1949, 62, 540-552.
56. An interchangeable pencil-type micromanipulator, *Science*, 1950, 111, 667-669.
57. Suggestions for determining the mobility of the stapes by means of an endoscope for the middle ear, *Laryngoscope*, 1950, 60, 97-110.
58. D-C potentials and energy balance of the cochlear partition, *J. Acoust. Soc. Amer.*, 1950, 22, 576-582 [32, 636-647].
59. (With W. A. Rosenblith), The mechanical properties of the ear, chap. 27 in S. S. Stevens (ed.), *Handbook of Experimental Psychology*, New York, John Wiley & Sons, Inc., 1951, pp. 1075-1115.
60. Microphonics produced by touching the cochlear partition with a vibrating electrode, *J. Acoust. Soc. Amer.*, 1951, 23, 29-35 [672-684].
61. The coarse pattern of the electrical resistance in the cochlea of the guinea pig (electro-anatomy of the cochlea), *J. Acoust. Soc. Amer.*, 1951, 23, 18-28 [36, 49-51, 654-672].
62. Resting potentials inside the cochlear partition of the guinea pig, *Nature*, 1952, 169, 241-242.
63. Micromanipulator with four degrees of freedom, *Trans. Amer. Microscopic Assoc.*, 1952, 71, 306-310.
64. D-C resting potentials inside the cochlear partition, *J. Acoust. Soc. Amer.*, 1952, 24, 72-76 [647-654].
65. Gross localization of the place of origin of the cochlear microphonics, *J. Acoust. Soc. Amer.*, 1952, 24, 399-409 [684-703].
66. Direct observation of the vibrations of the cochlear partition under a microscope, *Acta Oto-laryngol.*, 1952, 42, 197-201 [480-484].
67. Description of some mechanical properties of the organ of Corti, *J. Acoust. Soc. Amer.*, 1953, 25, 770-785 [34-35, 37-38, 485-500].
68. Shearing microphonics produced by vibrations near the inner and outer hair cells, *J. Acoust. Soc. Amer.*, 1953, 25, 786-790 [703-710].
69. Note on the definition of the term: hearing by bone conduction, *J. Acoust. Soc. Amer.*, 1954, 26, 106-107.
70. (With E. G. Wever and M. Lawrence), A note on recent developments in auditory theory, *Proc. Nat. Acad. Sci., U.S.*, 1954, 40, 508-512.
71. Some electro-mechanical properties of the organ of Corti, *Ann. of Otol. Rhinol. Laryngol.*, 1954, 63, 448.
72. Subjective cupulometry, *A.M.A. Arch. of Otolaryngol.*, 1955, 61, 16-28.
73. Paradoxical direction of wave travel along the cochlear partition, *J. Acoust. Soc. Amer.*, 1955, 27, 155-161 [510-524].
74. Human skin perception of traveling waves similar to those on the cochlea, *J. Acoust. Soc. Amer.*, 1955, 27, 830-841 [547-568].
75. Beitrag zur Frage der Frequenzanalyse in der Schnecke, *Archiv f. Ohr- usw. Heilk., u. Z. Hals- usw. Heilk.*, 1955, 167, 238-255.
76. Current status of theories of hearing, *Science*, 1956, 123, 779-783 [539-547].
77. Preparatory and air-driven micromanipulators for electrophysiology, *Rev. Sci. Instr.*, 1956, 27, 690-692 [40-49].

78. Simplified model to demonstrate the energy flow and formation of traveling waves similar to those found in the cochlea, *Proc. Nat. Acad. Sci., U.S.*, 1956, 42, 930-944 [524-534].
79. Sensations on the skin similar to directional hearing, beats, and harmonics of the ear, *J. Acoust. Soc. Amer.*, 1957, 29, 489-501 [568-590].
80. The ear, *Scientific Amer.*, 1957, 197, 66-78.
81. Neural volleys and the similarity between some sensations produced by tones and by skin vibrations, *J. Acoust. Soc. Amer.*, 1957, 29, 1059-1069 [590-609].
82. Funneling in the nervous system, *J. Acoust. Soc. Amer.*, 1958, 30, 399-412 [609-634].
83. Pendulums, traveling waves, and the cochlea, *Laryngoscope*, 1958, 68, 317-327.

REFERENCES

- Adrian, E. D. (1) *The Basis of Sensation*, New York, W. W. Norton & Company, Inc., 1928. (2) The microphonic action of the cochlea: An interpretation of Wever and Bray's experiments, *J. Physiol.*, 1931, 71, xxviii-xxix.
- Albert, K. Die Schwebung 15:16 im Innenohr nach Ort und Zeit, *Zeits. Biol.*, 1951, 104, 321-336.
- Alexander, Gustav, and Fischer, J. *Präparationstechnik des Gehörorgans*, Berlin, Urban & Schwarzenberg, 1925.
- Andrejew, N. Drei einfache Methoden der technischen Akustik, *Elektr. Nachr. Techn.*, 1931, 8, 488.
- Attwood, Stephen S. *Electric and Magnetic Fields*, 2d ed., New York, John Wiley & Sons, Inc., 1941.
- Backhaus, H. (1) Über Strahlungs- und Richtwirkungseigenschaften von Schallstrahlern, *Zeits. techn. Physik*, 1928, 9, 491-495. (2) Über die Schwingungsformen von Geigenkörpern, *Zeits. Physik*, 1930, 62, 143. (3) Über die Bedeutung der Ausgleichsvorgänge in der Akustik, *Zeits. Physik*, 1932, 13, 31.
- Ballantine, S. (1) Effect of diffraction around the microphone in sound measurements, *Phys. Rev.*, 1928, 32, 988. (2) Effect of cavity resonance on the frequency response characteristic of the condenser microphone, *Proc. Inst. Radio Engrs.*, 1930, 18, 1206-1215.
- Bárány, E. (1) A contribution to the physiology of bone conduction, *Acta Otolaryngol.*, 1938, suppl. 26. (2) Hearing, *Ann. Rev. Physiol.*, 1941, 3, 449.
- Bárány, R. Beziehungen zwischen Vestibularapparat und Cerebellum, *Verhandl. deutsch. otolog. Gesellsch.*, 1910, 81.
- Barkhausen, H. Ein neuer Schallmesser für die Praxis, *Zeits. techn. Physik*, 1926, 7, 599.
- Barkhausen, H., and Lewicki, G. Vorträge und Diskussionen von der 88 Versammlung deutscher Naturforscher und Ärzte in Innsbruck, *Phys. Zeits.*, 1924, 25, 537.
- Barlow, H. B. Summation and inhibition in the frog's retina, *J. Physiol.*, 1953, 119, 69-88.
- Barlow, H. B., Fitzhugh, R., and Kufler, S. W. Change of the organization in the receptive fields of the cat's retina during dark adaptation, *J. Physiol.*, 1957, 137, 338-354.
- Bartlett, F. C., and Mark, H. A note on local fatigue in the auditory system, *Brit. J. Psychol.*, 1922, 13, 215-218.
- Beatty, R. T. *Hearing in Man and Animals*, London, G. Bell & Sons, Ltd., 1932.
- Beljers, H. J. *Tijdschr. nederl. radiogenoots.*, 1934, 6, 115.
- Benecke, H. Über die günstigste Raumdämpfung, *Ann. Physik*, 1932, 5, 259.
- Berendes, Z. Die Spannung der menschlichen Basilarmembran, *Zeits. Hals- Nasen-Ohrenheilk.*, 1934, 36, 338-342.
- Berger, R. (1) Über Erschütterungen, *Gesundheits Ingenieur*, 1913, 433. (2) Die Abwehr von Lärm und Erschütterungen, in W. Wien and F. Harms, *Handbuch der experimentellen Physik*, Leipzig, Akademische Verlagsgesellschaft m.b.H., 1934, 17, part 3, 7-8.
- Bernamont, J. (1) Fluctuations de résistance dans un conducteur métallique de faible volume, *Compt. Rend. Acad. Sci., Paris*, 1934, 198, 1755. (2) Étude expérimentale des fluctuations de résistance dans un conducteur métallique de volume, *Compt. Rend. Acad. Sci., Paris*, 1934, 198, 2144.

- Birkhoff, G. *Hydrodynamics, a Study in Logic, Facts, and Similitude*, Princeton, N.J., Princeton University Press, 1950.
- Bleeker, J. D., and De Vries, Hl. The microphonic activity of the labyrinth of the pigeon, I, The cochlea, *Acta Oto-laryngol.*, 1949, 37, 289-297.
- Böhme, H. Dynamisches Verhalten von Schalldämmstoffen, *Akust. Zeits.*, 1937, 2, 303.
- Bogert, B. P. Determination of the effects of dissipation in the cochlear partition by means of a network representing the basilar membrane, *J. Acoust. Soc. Amer.*, 1951, 23, 151-154.
- Bolton, T. L. Rhythm, *Amer. J. Psychol.*, 1894, 6, 145-238.
- Bonnier, P. De la nature des phénomènes auditifs, *Bull. Sci. du Nord.*, 1895, 25, 267-297.
- Braunmühl, H. J. von. Fernübertragung auf drahtlosem Wege, in W. Wien and F. Harms, *Handbuch der experimentellen Physik*, Leipzig, Akademische Verlagsgesellschaft m.b.H., 1934, part 3, 17, 270-312.
- Brecher, G. A. Die untere Hör- und Tongrenze, *Pflüg. Arch. ges. Physiol.*, 1934, 234, 380-393.
- Breisig, Franz. *Lehrbuch der theoretischen Telegraphie*. Brunswick, Germany, Vieweg-Verlag, 1910.
- Breuer, Carl. *Kitte und Klebstoffe*, Leipzig, 1922.
- Breuer, J. Über die Funktion der Otolithen-Apparate, *Pflüg. Arch. ges. Physiol.*, 1891, 48, 195-306.
- Brillouin, L. Fluctuations de courant dans un conducteur, *Helv. phys. Acta*, 1934, 7, 47.
- Brintzer, W. Die Unterschiedsempfindlichkeit für Lautstärke bei Gehörkrankungen; Versuche mit dem Otoaudion, *Monatsschr. Ohrenheilk.*, 1935, 69, 1301-1321.
- Broom, R. (1) On the fate of the quadrate bone in mammals, *Ann. and Mag. Nat. Hist.*, 1890, 2, 409. (2) On the structure of the internal ear and the relations of the basicranial nerves in Diconodon, and on the homology of the mammalian auditory ossicles, *Proc. Zool. Soc. London*, 1912, 1, 419.
- Bruïne-Altes, J. C. de. *The Symptom of Regression in Different Kinds of Deafness*, Dissertation, Groningen, 1946.
- Buchthal, F. Ein neuer Mikromanipulator mit Zusatzgeräten (Mikromesser und unpolarisierbare Mikroelektroden), *Zeits. wiss. Mikr.*, 1941-1942, 58, 126.
- Buchthal, F., and Persson, C. R. A micromanipulative apparatus, *J. sci. Instr.*, 1936, 13, 20.
- Budde, E. (1) Über die Resonanztheorie des Hörens, *Phys. Zeits.*, 1917, 18, 225-236, 249-260. (2) Mathematische Theorie der Gehörsempfindung, in E. Abderhalden's *Handbuch der biologischen Arbeitsmethoden*, Berlin, Urban & Schwarzenberg, 1937, Abt. 5, Teil 7, Heft 1, 175.
- Burlet, H. M. de. Zur vergleichenden Anatomie und Physiologie des perilymphatischen Raumes, *Acta Oto-laryngol.*, 1929, 13, 152.
- Burr, H. S. Field properties of the developing frog's egg, *Proc. Nat. Acad. Sci. U.S.*, 1941, 27, 276.
- Bush, V. The differential analyzer: A new machine for solving differential equations, *J. Franklin Inst.*, 1931, 212, 447.
- Carson, J. R. *Electrical Circuit Theory and the Operational Calculus*, New York, McGraw-Hill Book Company, Inc., 1926.
- Chambers, R., and Kopac, M. J. In C. E. McClung's *Handbook of Microscopical Technique*, New York, Paul B. Hoeber, Inc., 1937.
- Chapin, E. K., and Firestone, F. A. Influence of phase on quality and loudness: The interference of subjective harmonics, *J. Acoust. Soc. Amer.*, 1934, 5, 173-180.
- Chocholle, R., and Legoux, J. P. Facteurs intervenant dans la mesure des distorsions présentées par les potentiels microphoniques cochléaires, *J. de Physiol.*, 1956, 48, 448-449.
- Cole, K. S., and Curtis, H. J. Electrical impedance of nerve during activity, *Nature*, 1938, 142, 209.

- Coradi, G. *Der Harmonische Analysator*, Zürich, 1894.
- Corti, A. Recherches sur l'organe de l'ouïe des mammifères, *Zeits. wiss. Zool.*, 1851, 3, 109-169.
- Cotton, J. C. Resonance in soft-walled cylinders, *J. Acoust. Soc. Amer.*, 1934, 5, 208.
- Crandall, I. B. *Theory of Vibrating Systems and Sound*, Princeton, N.J., D. Van Nostrand Company, Inc., 1926.
- Crowe, S. J., Guild, S. R., and Polvogt, L. M. Observations on the pathology of high-tone deafness, *Bull. Johns Hopkins Hosp.*, 1934, 54, 315-379.
- Dahmann, H. (1) Zur Physiologie des Hörens, *Zeits. Hals- Nasen- Ohrenheilk.*, 1929, 24, 462-497. (2) Zur Physiologie des Hörens, *Zeits. Hals- Nasen- Ohrenheilk.*, 1930, 27, 329-368.
- Davis, H. The electrical phenomena of the cochlea and the auditory nerve, *J. Acoust. Soc. Amer.*, 1935, 6, 205-215.
- Davis, H., Derbyshire, A. J., Lurie, M. H., and Saul, L. J. The electric response of the cochlea, *Amer. J. Physiol.*, 1934, 107, 311-332.
- Davis, H., Fernández, C., and MacAuliffe, D. R. The excitatory process in the cochlea, *Proc. Nat. Acad. Sci., U.S.*, 1950, 36, 580-587.
- Davis, H., Gernandt, B. E., Riesco-MacClure, J. S., and Covell, W. P. Aural microphonics in the cochlea of the guinea pig, *J. Acoust. Soc. Amer.*, 1949, 21, 502-510.
- Davis, H., and Saul, L. J. Action currents in the auditory tracts of the midbrain of the cat, *Science*, 1931, 74, 105.
- Denker, Alfred, and Kahler, O. (eds.). *Handbuch der Hals- Nasen- Ohrenheilkunde*, vol. 6, *Die Krankheiten des Gehörorgans*, part 1, Berlin, Springer-Verlag, 1926.
- De Vries, Hl. (1) Minimum perceptible energy and Brownian motion in sensory processes, *Nature*, 1948, 161, 63. (2) Brownian movement and hearing, *Physica*, 1948, 14, 48-60. (3) Die Reizschwelle der Sinnesorgane als physikalisches Problem, *Experientia*, 1948, 4, 205-213. (4) The minimum audible energy, *Acta Oto-laryngol.*, 1948, 36, 230-235. (5) Struktur und Lage der Tektorialmembran in der Schnecke, untersucht mit neueren Hilfsmitteln, *Acta Oto-laryngol.*, 1949, 37, 334-338.
- Diestel, H. G. Akustische Messungen an einem mechanischen Modell des Innenohres; Ein Beitrag zur Hydrodynamik der Cochlea, *Acustica*, 1954, 4, 489.
- Dietsch, G., and Fricke, W. Ein photoelektrisch-mechanisches Verfahren zur harmonischen Analyse periodischer Funktionen, *Elektr. Nachr. Techn.*, 1932, 9, 341.
- Dijkgraaf, S. (1) Über den Temperatursinn der Fische, *Zeits. vergl. Physiol.*, 1940, 27, 587. (2) Bau und Funktionen der Seitenorgane und des Ohrlabyrinths bei Fischen, *Experientia*, 1952, 8, 205.
- Doty, H. A. The flexibility of diatom shells, *J. appl. Micr. lab. Meth.*, 1900, 3, 991.
- DuVerney, Joseph Guichard. *Traité de l'organe de l'ouïe*, Paris, 1683; Leiden, 1731, 91.
- Egan, J. P., and Klumpp, R. G. The error due to masking in the measurement of aural harmonics by the method of best beats, *J. Acoust. Soc. Amer.*, 1951, 23, 275-286.
- Emmermann, C. *Leica-Technik*, Halle, Germany, W. Knapp Verlag, 1934.
- Engstrom, H. Microscopic anatomy of the inner ear, *Acta Oto-laryngol.*, 1951, 40, 5-22.
- Esser, M. H. M. The mechanism of the middle ear, *Bull. math. Biophys.*, 1947, 9, 29-40, 75-91.
- Ewald, J. R. (1) Zur Physiologie des Labyrinths, VI, Eine neue Hörtheorie, *Pflüg. Arch. ges. Physiol.*, 1899, 76, 147-188. (2) Zur Physiologie des Labyrinths, VII, Die Erzeugung von Schallbildern in der Camera acustica, *Pflüg. Arch. ges. Physiol.*, 1903, 93, 485-500. (3) Bemerkungen zur Schallbildertheorie, *Zentralbl. Physiol.*, 1914, 28, 756.
- Ewald, J. R., and Jäderholm, G. A. Die Herabsetzung der subjektiven Tonhöhe durch Steigerung der objektiven Intensität, *Pflüg. Arch. ges. Physiol.*, 1908, 124, 29.
- Exner, S. Zur Lehre von den Gehörsempfindungen, *Pflüg. Arch. ges. Physiol.*, 1876, 13, 228-253.

- Eyring, C. F. Reverberation time in "dead" rooms, *J. Acoust. Soc. Amer.*, 1930, 1, 217-241.
- Fahrendholz, S., Kluge, J., and Linckh, H. E. Über neue Quartzdruckmesskammern für das piezoelektrische Messverfahren, I, *Phys. Zeits.*, 1937, 38, 73.
- Fechner, Gustav T. *Elemente der Psychophysik*, 2d ed., Leipzig, Von Breitkopf & Härtel, 1889.
- Firestone, F. A. (1) New analogy between mechanical and electrical systems, *J. Acoust. Soc. Amer.*, 1933, 4, 249. (2) The mobility method of computing the vibration of linear mechanical and acoustical systems: Mechanical-electrical analogies, *J. appl. Physics*, 1938, 9, 373.
- Fischer, M. H. Die Regulationsfunktionen des menschlichen Labyrinthes und die Zusammenhänge mit verwandten Funktionen, *Ergebn. Physiol.*, 1928, 27, 209-379.
- Fischer, O. Über ein von Max Wein geäußertes Bedenken gegen die Helmholtzsche Resonanztheorie des Hörens, *Ann. Physik*, 1908, 25, 118-134.
- Flanders, P. B. Method of measuring acoustic impedance, *J. Acoust. Soc. Amer.*, 1932, 4, 402-410.
- Fletcher, H. (1) Physical measurements of audition and their bearing on the theory of hearing, *J. Franklin Inst.*, 1923, 196, 189-326. (2) *Speech and Hearing*, Princeton, N.J., D. Van Nostrand Company, Inc., 1929. (3) A space-time pattern theory of hearing, *J. Acoust. Soc. Amer.*, 1930, 1, 311-343. (4) Symposium on wire transmission of symphonic music—reports in auditory perspective: Basic requirements, *Electr. Engng.*, 1934, 53, 9. (5) Auditory patterns, *Revs. mod. Physics*, 1940, 12, 47-65. (6) On the dynamics of the cochlea, *J. Acoust. Soc. Amer.*, 1951, 23, 637-645.
- Fletcher, H., and Munson, W. A. Loudness, its definition, measurement and calculation, *J. Acoust. Soc. Amer.*, 1933, 5, 82-108.
- Fowler, E. P. (1) Marked deafened areas in normal ears, *Arch. Otolaryngol.*, 1928, 8, 151-155. (2) A method for the early detection of otosclerosis: A study of sounds well above threshold, *Arch. Otolaryngol.*, 1936, 24, 731. (3) The diagnosis of diseases of the neural mechanism of hearing by the aid of sounds well above threshold, *Laryngoscope*, 1937, 47, 289.
- Frank, O. Die Leitung des Schalles im Ohr, *Sitzungsber. Akad. Wiss., München, math.-phys. Kl.*, 1923, 53, 11-77.
- French, N. R., and Steinberg, J. C. Factors governing the intelligibility of speech sounds, *J. Acoust. Soc. Amer.*, 1947, 19, 90-119.
- Frey, M. v. Die Tangorezeptoren des Menschen, in A. Bethe (ed.), *Handbuch der normalen und pathologischen Physiologie*, 11, *Receptionsorgane I*, Berlin, Springer-Verlag, 1926, 97.
- Frey, M. v., and Goldman, A. Der zeitliche Verlauf der Einstellung bei den Druckempfindungen, *Zeits. Biol.*, 1914, 65, 183.
- Frocht, Max. *Photoelasticity*, New York, John Wiley & Sons, Inc., 1941.
- Fumagalli, Z. Ricerche morfologiche sull'apparato di trasmissione del suono, *Arch. ital. Otol. Rinol. Laringol.*, 1949, 60, suppl. 1.
- Galambos, R. Suppression of the auditory nerve activity by stimulation of efferent fibers to the cochlea, *J. Neurophysiol.*, 1956, 19, 424-437.
- Garten, S. Beiträge zur Vokallehre, I, Analyse der Vokale mit dem Quinckeschen Interferenzapparat, *Abhandl. Sächs. Akad. Wiss., Leipzig, math.-phys. Kl.*, 1921, 38, no. 7.
- Gatty, O., and Rawdon-Smith, A. F. Origin of the cochlear effect, *Nature*, 1937, 139, 670.
- Geffcken, W. Untersuchungen über Schwellenwerte, III, Über die Bestimmung der Reizschwelle der Hörempfindung aus Schwellendruck und Trommelfellimpedanz, *Ann. Physik*, 1934, 19, 829-848.
- Geffcken, W., and Keibs, L. Über die Bestimmung der Reizschwelle der Hörempfindung aus Schwellendruck und Trommelfellimpedanz, *Ann. Physik*, 1933, 16, 404.
- Geiger, P. H., and Firestone, F. A. The estimation of fractional loudness, *J. Acoust. Soc. Amer.*, 1933, 5, 26.

- Geldard, F. A. (1) The perception of mechanical vibration, *J. gen. Psychol.*, 1940, 22, 243-308. (2) Hearing through the skin, *Research Revs.*, October, 1954.
- Gerdien, H., Pauli, H., and Trendelenburg, F. Untersuchungen über Erschütterungsschwingungen und Geräusche, *Zeits. techn. Physik*, 1929, 10, 374.
- Gerlach, E. Messung von Schall-Druckamplituden, *Wiss. Veröffentlich. Siemens-Konzern*, 1923, 3, 139.
- Gildemeister, M. Probleme und Ergebnisse der neueren Akustik, *Zeits. Hals- Nasen- Ohrenheilk.*, 1930, 27, 299-328.
- Goldberg, E. Herstellung von starken Verkleinerungen, *Zeits. techn. Physik*, 1926, 7, 500.
- Gray, A. A. On a modification of the Helmholtz theory of hearing, *J. Anat. Physiol.*, 1900, 34, 324-350.
- Gray, T. S. A photoelectric integrator, *J. Franklin Inst.*, 1931, 212, 77.
- Grimm, K. Der Einfluss der Zeitform auf die Wahrnehmung der Zeitdauer, *Zeits. Psychol.*, 1934, 132, 104.
- Guild, S. R. Correlations of histologic observations and the acuity of hearing, *Acta Oto-laryngol.*, 1932, 17, 207-249.
- Haas, H. Über den Einfluss eines Einfachechos auf die Hörsamkeit von Sprache, *Acustica*, 1951, 1, 49-58.
- Hähnle, W. Die Darstellung elektromechanischer Gebilde durch rein elektrische Schaltbilder, *Wiss. Veröffentlich. Siemens-Konzern*, 1932, 11, 1.
- Hahnemann, W., and Hecht, H. (1) Der mechanisch-akustische Aufbau eines Telephons, *Ann. Phys. Chem.*, 1919, 60, 454-480. (2) Entgegnung auf die Bemerkung von M. Wien zu unserer Arbeit; Der mechanisch-akustische Aufbau eines Telephons, *Ann. Phys. Chem.*, 1921, 64, 671.
- Hallpike, C. S., Hood, J. D., and Byford, G. H. The design, construction and performance of a new type of revolving chair, *Acta Oto-laryngol.*, 1952, 42, 511-538.
- Hallpike, C. S., and Rawdon-Smith, A. F. (1) The Helmholtz resonance theory of hearing, *Nature, London*, 1934, 133, 614. (2) The origin of the Wever and Bray phenomenon, *J. Physiol.*, 1934, 83, 243. (3) The Wever and Bray phenomenon: A summary of the data concerning the origin of the cochlear effect, *Ann. Otol. Rhinol. Laryngol.*, 1937, 46, 976.
- Hardesty, I. On the nature of the tectorial membrane and its probable role in the anatomy of hearing, *Amer. J. Anat.*, 1908, 8, 109-179.
- Harris, J. D., and Meyers, C. K. The emergence of a tonal sensation, *J. exper. Psychol.*, 1949, 39, 228-237.
- Hartline, H. K. The receptive fields of optic nerve fibers, *Amer. J. Physiol.*, 1940, 130, 690-699.
- Hartmann-Kempf, R. Direkt zeigender Frequenzmesser für Frequenzen bis ca. 1500 Perioden per Sekunde, *Phys. Zeits.*, 1910, 11, 1183.
- Hartridge, H. A vindication of the resonance hypothesis of audition, *Brit. J. Psychol.*, 1921, 12, 142-146.
- Hasse, Carl. Die vergleichende Morphologie und Histologie des häutigen Gehörorganes der Wirbelthiere, *Anat. Stud.*, 1873, 1.
- Hausmann, T. Neue und endgültige Belege für das Vorhandensein einer tiefen Druckempfindung, *Zeits. Biol.*, 1933, 94, 264.
- Hecht, H., and Fischer, F. A. In W. Wien and F. Harms, *Handbuch der Experimentellen Physik, Technische Akustik*, Leipzig, Akademische Verlagsgesellschaft m.b.H., 1934, 17, part 2, 308.
- Held, H. Die Cochlea der Säuger und der Vögel, in A. Bethe (ed.), *Handbuch der normalen und pathologischen Physiologie*, 11, *Receptionsorgane I*, Berlin, Springer-Verlag, 1926, 467.
- Held, H., and Kleinknecht, F. Die lokale Entspannung der Basilarmembran und ihre Hörlücken, *Pflüg. Arch. ges. Physiol.*, 1927, 216, 1-31.
- Helmholtz, H. L. F. (1) *Die Lehre von den Tonempfindungen als physiologische Grundlage für die Theorie der Musik*, 1st ed., Brunswick, Germany, Vieweg-Verlag, 1863; Eng. trans. by A. J. Ellis, *On the sensations of tone*, 2d Eng. ed., 1885. (2) Über die Mechanik der Gehörknöchelchen und des Trommelfells,

- Pflüg. Arch. ges. Physiol., 1868, 1, 1-60. (3) Studien über electrische Grenzschichten, *Ann. Physik.*, 1879, 7, 337.
- Hensen, V. (1) Zur Morphologie der Schnecke des Menschen und der Säugetiere, *Zeits. wiss. Zool.*, 1863, 13, 481-512. (2) Die Fortschritte in einigen Teilen der Physiologie des Gehörs, *Ergebn. Physiol.*, 1902, 2, 848-895.
- Herzog, H. Die Mechanik der Knochenleitung im Modellversuch, *Zeits. Hals-Nasen-Ohrenheilk.*, 1930, 27, 402-408.
- Hilding, A. C. Studies on the otic labyrinth, I, On the origin and insertion of the tectorial membrane; II, A theory on the stimulation of the organ of Corti by sound vibrations, *Ann. Otol. Rhinol. Laryngol.*, 1952, 61, 354-383.
- Holst, E. v. (1) Personal communication, June, 1949. (2) Die Arbeitsweise des Statolithenapparates bei Fischen, *Zeits. vergl. Physiol.*, 1950, 32, 60-120. (3) Die Tätigkeit des Statolithenapparates im Wirbeltierlabyrinth, *Naturwissenschaften*, 1950, 37, 265-272.
- Hornbostel, E. M. v. (1) Beobachtungen über ein- und zweiohriges Hören, *Psychol. Forsch.*, 1923, 4, 64. (2) Neue Beiträge zur physiologischen Hörtheorie, *Jahresber. Phys. exp. Pharmacol.*, 1928, 9, 753. (3) Das räumliche Hören, in A. Bethe (ed.), *Handbuch der normalen und pathologischen Physiologie*, Berlin, Springer-Verlag, 1926, 11, 602-618.
- Hornbostel, E. M. v., and Wertheimer, M. Ueber die Wahrnehmung der Schallrichtung, *Sitzungber. Akad. Wiss.*, Berlin, 1920, 15, 388-396.
- Hort, W., and Thoma, A. *Die Differentialgleichungen der Technik und Physik*, 3d ed., Munich, Johann Ambrosius Barth, 1939, 364.
- Howe, H. A., and Guild, S. R. Absence of the organ of Corti and its possible relation to electric auditory nerve responses [Abstract], *Anat. Rec.*, 1933, 55, 20-21.
- Huggins, W. H., and Licklider, J. C. R. Place mechanisms of auditory frequency analysis, *J. Acoust. Soc. Amer.*, 1951, 23, 290-299.
- Huizing, H. C. (1) *Audiometrie*, 1941. (2) De Regressiefactor en zijn beteekenis bij het functioneele gehooronderzoek en de gehoorprothese, *Neder. Tijds. Geneesk.*, 1941, 85, 4529.
- Hunt, R. S. Damping and selectivity of the inner ear, *J. Acoust. Soc. Amer.*, 1942, 14, 50-57.
- Hurst, C. H. A new theory of hearing, *Trans. Liverpool Biol. Soc.*, 1895, 9, 321-353. "Hülle," *Des Ingenieurs Taschenbuch*, 24 Aufl., Berlin, W. Ernst und Sohn, 1923, 1, 719.
- Janovsky, W. (1) Ueber die Hörbarkeit von Verzerrungen, *Elektr. Nachr. Techn.*, 1929, 6, 421-439. (2) Über den Zusammenhang zwischen Schallempfindung und Schallreiz und seinen Einfluss auf die Hörbarkeit von Verzerrungen, *Zeits. techn. Physik*, 1931, 12, 611.
- Janovsky, W., and Spandöck, F. Aufbau und Untersuchung eines Schallgedämpften Raumen, *Akust. Zeits.*, 1937, 2, 322.
- Jielof, R., Spoor, A., and De Vries, Hl. The microphonic activity of the lateral line, *J. Physiol.*, 1952, 116, 137-157.
- Johnson, K. S. *Transmission Circuits for Telephonic Communication*, Princeton, N.J., D. Van Nostrand Company, Inc., 1924.
- Jones, I. H., and Knudsen, V. O. Audiometry and the prescribing of hearing aids, *Laryngoscope*, 1936, 46, 523.
- Jung, H. Untersuchungen zu den Theorien des Hörens, *Akust. Zeits.*, 1940, 5, 268-283.
- Kato, T. Zur Physiologie der Binnenmuskeln des Ohres, *Pflüg. Arch. ges. Physiol.*, 1913, 150, 569-625.
- Katsuki, Y., and Covell, W. P. The organ of Corti by phase contrast microscopy, *Laryngoscope*, 1953, 63, 1.
- Katz, D. Methoden der Untersuchung des Vibrationssinnes, in E. Abderhalden's *Handbuch der biologischen Arbeitsmethoden*, Berlin, Urban & Schwarzenberg, 1937, Abt. 5, Teil 7, 879-918.
- Keidel, W. D. (1) Messung der Hautwellengeschwindigkeiten bei Vibrationsreizen am Menschen, *Pflüg. Arch. ges. Physiol.*, 1952, 255, 213-227. (2) Aktionspotentiale des N. dorsocutaneus bei niederfrequenter Vibration der Froschrückenhaut,

- Pflüg. Arch. ges. Physiol.*, 1955, 260, 416-436. (3) *Vibrationsreceptoren; Der Erschüngssinn des Menschen*, Erlangen, Universitätsbund, 1956.
- Keidel, W. D., and Schmidt, H. G. Hautwellenlängen und dynamischer Scherelastizitätskoeffizient der menschlichen Körperoberfläche bei Vibrationen mit 50 Hz, *Pflüg. Arch. ges. Physiol.*, 1955, 260, 274-291.
- Kerekes, G. Klinisch-experimentelle Untersuchungen über die Beziehungen zwischen endolabyrinthärem Druck und Hörfunktion, *Zeits. Hals- Nasen- Ohrenheilk.*, 1927, 18, 458-468.
- Kessel, J. Ueber das Hören von Tönen und Geräuschen, *Arch. Ohrenheilk.*, 1882, 18, 136-151.
- Kingsbury, B. A. A direct comparison of the loudness of pure tones, *Phys. Rev.*, 1927, 29, 373, 588-600.
- Kircher, Athanasius. *Misurgia Universalis*, Romae, 1650.
- Kleinknecht, F. Methoden zur Erforschung des Kochlearapparates, in E. Abderhalden's *Handbuch der biologischen Arbeitsmethoden*, Berlin, Urban & Schwarzenberg, 1937, Abt. 5, Teil 7, Heft 11, 1541-1660.
- Klemm, O. Über die Wirksamkeit kleinster Zeitunterschiede auf dem Gebiete des Tastsinns, *Arch. ges. Psychol.*, 1925, 50, 205-220.
- Knudsen, Vern O. (1) The sensibility of the ear to small differences in intensity and frequency, *Phys. Rev.*, 1923, 21, 84-103. (2) "Hearing" with the sense of touch, *J. gen. Psychol.*, 1928, 1, 320-352. (3) Hearing of speech in auditoriums, *J. Acoust. Soc. Amer.*, 1929, 1, 56-82. (4) Resonance in small rooms, *J. Acoust. Soc. Amer.*, 1932, 4, 20. (5) *Architectural Acoustics*, New York, John Wiley & Sons, Inc., 1932. (6) Recent developments in architectural acoustics, *Rev. mod. Phys.*, 1934, 6.
- Knudsen, Vern, O., and Jones, I. H. Bone conduction, *Arch. Otolaryngol.*, 1931, 13, 489-505.
- Kobrak, H. G. Round window membrane of the cochlea, *Arch. Otolaryngol.*, 1949, 49, 36-47.
- Köhler, W. (1) Akustische Untersuchungen I, *Zeits. Psychol.* 1909, 54, 241-289. (2) Zur Theorie des Sukzessivvergleichs und der Zeitfehler, *Psychol. Forsch.*, 1923, 4, 115-175.
- Kölliker, Albert. (1) Über den Bau und die Verbreitung der glatten Muskeln, *Zeits. wiss. Zool.*, 1849, 1, 55. (2) *Mikroskopische Anatomie oder Gewebelehre des Menschen*, Leipzig, W. Englemann, 1852, 2, 749.
- Kohler, I. Über Aufbau und Wandlungen der Wahrnehmungswelt, *Sitzber. Osterr. Akad. Wiss., philos.-hist. Kl.*, 1951, 227, Abt. 1, 177.
- Kolmer, W. (1) Der Bau der Endapparate des Nervus octavus und deren physiologische Deutung, *Ergebn. Physiol.*, 1911, 11, 372. (2) Mikroskopische Anatomie des Nervösen Apparates des Ohres, in G. Alexander and O. Marburg's *Handbuch der Neurologie des Ohres*, Berlin-Vienna, Urban & Schwarzenberg, 1924, I, part 1, 101.
- Krause, W. Allgemeine und microscopische Anatomie, in Carl F. T. Krause's *Handbuch der menschlichen Anatomie*, 1927, I.
- Kucharski, P. Schwingungen von Membranen in einer pulsierenden Flüssigkeit (Ein Beitrag zur Resonanztheorie des Hörens), *Phys. Zeits.*, 1930, 31, 264-280.
- Kühl, A. Über den Einfluss des Grenzkontrastes auf Präzisionsmessungen, *Phys. Zeits.*, 1928, 29, 1.
- Kuffler, S. W. Discharge patterns and functional organization of mammalian retina, *J. Neurophysiol.*, 1953, 16, 37-68.
- Kuhl, Walter. Ueber die Abhängigkeit der Lautstärke des subjektiven Differenztones von der Frequenz der Primärtöne, *Akust. Zeits.*, 1939, 4, 43-50.
- Kuile, E. ter. (1) Die Übertragung der Energie von der Grundmembran auf die Haarzellen, *Pflüg. Arch. ges. Physiol.*, 1900, 79, 146-157. (2) Die richtige Bewegungsform der Membrana basilaris, *Pflüg. Arch. ges. Physiol.*, 1900, 79, 484-509.
- Kupfer, E. On the origin of the Wever-Bray response and on an electrotherapy of the ear, *J. Laryng., London*, 1938, 53, 16-31.

- Kurtz, R. Zur Messung von Absorptions- und Empfindlichkeitskurven des menschlichen Ohrs, *Akust. Zeits.*, 1938, 3, 74-79.
- Landes, G. Zur Physik der normalen Lungenperkussion, *Deutsch. Arch. klin. Med.*, 1939, 185, 116-133.
- Lane, C. E. Binaural beats, *Phys. Rev.*, 1925, 26, 401-412.
- Lange, B. *Die Photoelemente und ihre Anwendungen*, Munich, Johann Ambrosius Barth, 1936.
- Langenbeck, B. (1) Experimentelles und Theoretisches zur Frage der Hörschwellenbestimmung, *Pflüg. Arch. ges. Physiol.*, 1931, 226, 11-46. (2) Das Symmetriegesetz der erblichen Taubheit, *Zeits. Hals- Nasen- Ohrenheilk.*, 1936, 39, 223-261.
- Lawrence, M., and Yantis, P. A. Onset and growth of aural harmonics in the over-loaded ear, *J. Acoust. Soc. Amer.*, 1956, 28, 852-858.
- Legoux, J. P., Chochole, R., and Wisner, A. Modifications de la distorsion observée sur le potentiel microphonique cochléaire pendant l'anoxie, *J. de Physiol.*, 1956, 48, 605-607.
- Lehmann, Alfred. *Die körperlichen Äusserungen psychischer Zustände*, trans. by F. Bendixen, 1905.
- Lehner, Sigmund. *Kitte und Klebstoffe*, Vienna, 1932.
- Lewis, D. Support for the exploring tone method of measuring aural harmonics, *Psychol. Rev.*, 1940, 47, 169-183.
- Lichte, H. Energieabsorption in Schallantennen erster Ordnung, *Phys. Zeits.*, 1918, 19, 19.
- Licklider, J. C. R. Hearing, *Ann. Rev. Psychol.*, 1953, 4, 89-110.
- Lifschitz, S. (1) Optimum reverberation for an auditorium, *Phys. Rev.*, 1925, 25, 391. (2) Mean intensity of sound in an auditorium and optimum reverberation, *Phys. Rev.*, 1926, 27, 618. (3) Acoustics of large auditoriums, *J. Acoust. Soc. Amer.*, 1932, 4, 112.
- Lincke, Carl Gustav. *Handbuch der theoretischen und praktischen Ohrenheilkunde*, I, Leipzig, 1837.
- Ling, G., and Gerard, R. W. The normal potential of frog sartorius fibers, *J. Cell. Comp. Physiol.*, 1949, 34, 383-396.
- Lippmann, G. Expériences électrocapillaires, *J. de Phys. Radium*, 1874, 3, ser. 1, 41.
- Lohmann, W. Die hermannschen Schablonen zur harmonischen Analyse, *Zeits. angew. Math. Mech.*, 1922, 2, 153.
- Lowy, K. (1) Cancellation of the electrical cochlear response with air-conducted and bone-conducted sound, *J. Acoust. Soc. Amer.*, 1942, 14, 156-158. (2) Physiological demonstration of a property of the inner ear predicated by Békésy's model, *J. Acoust. Soc. Amer.*, 1951, 23, 716.
- Lux, F. Ueber die Resonanztheorie des Hörens, reported by E. Budde, *Phys. Zeits.*, 1917, 18, 225-236, 249-260.
- McClung, C. E. *Handbook of Microscopical Technique*, New York, Paul B. Hoeber, Inc., 1937.
- Mach, Ernst. (1) Zur Theorie des Gehörorgans, *Sitzungsber. Akad. Wiss., Wien, math.-nat. Kl.*, 1863, Abt. 2, 48, 283-300. (2) Ueber die physiologische Wirkung räumlich vertheilter Lichtreize, *Sitzungsber. Akad. Wiss., Wien, math.-nat. Kl.*, 1864, Abt. 2, 57, 11. (3) Ueber den physiologischen Effect räumlich vertheilter Lichtreize, *Sitzungsber. Akad. Wiss., Wien, math.-nat. Kl.*, 1866, Abt. 2, 54, 131. (4) *Beitrag zur Analyse der Empfindungen*, 1886.
- Mach, Ernst, and Kessel, J. Die Funktion der Trommelhöhle und der Tuba Eustachii, *Sitzungsber. Akad. Wiss., Wien, math.-phys. Kl.*, 1872, Abt. 3, 66, 337-343.
- MacNair, W. A. Optimum reverberation time for auditoriums, *J. Acoust. Soc. Amer.*, 1930, 1, 242-248.
- Mader, O. Ein einfacher harmonischer Analysator mit beliebiger Basis, *Elektrotechn. Zeits.*, 1909, 30, 847.
- Mangold, E. Das äussere und das mittlere Ohr und ihre physiologischen Funktionen, in A. Bethe (ed.), *Handbuch der normalen und pathologischen Physiologie*, Berlin, Springer-Verlag, 1926, 11, 406-435.

- Maré, G. de. Audiometrische Untersuchungen über das Verhalten des normalen und schwerhörigen Ohres bei funktioneller Belastung, nebst Bemerkungen zur Theorie des Gehörs, *Acta Oto-laryngol.*, 1939, suppl. 31.
- Marks, L. S. (ed.). *Mechanical Engineers' Handbook*, New York, McGraw-Hill Book Company, Inc., 4th ed., 1941, 455, 461, 477.
- Markus, John, and Zeff, V. *Electronics for Engineers*, New York, McGraw-Hill Book Company, Inc., 1945, 12.
- Martin, H. Über Tonhöhe und Dämpfung der Schwingungen von Saiten in verschiedenen Flüssigkeiten, *Ann. Physik*, 1925, 77, 727.
- Maxfield, T. Acoustic control of recording for talking motion pictures, *Trans. Soc. Motion Pict. Engr.*, 1930, 14, 85.
- Mayer, O. Das anatomische Substrat der Altersschwerhörigkeit, *Arch. Ohren-Nasen-Kehlkopfheilk.*, 1919, 105, 1-13.
- Metz, O. The acoustic impedance measured on normal and pathological ears, *Acta Oto-laryngol.*, 1946, suppl. 63.
- Meyer, E. (1) Beiträge zur Untersuchung des Nachhalles, *Elektr. Nachr. Techn.*, 1927, 4, 135. (2) Das Gehör, in H. Geiger and K. Scheel's *Handbuch der Physik*, Berlin, Springer-Verlag, 1927, 8. (3) Ein neues automatisches Verfahren der Nachhallmessung, *Zeits. techn. Physik*, 1930, 11, 253. (4) Schalltechnische Eigenschaften des Flachglases, *Glastechnische Ber.*, 1932, Ber. 10, 4, 200. (5) Akustische Messtechnik, in W. Wien and F. Harms, *Handbuch der experimentellen Physik*, Leipzig, Akademische Verlagsgesellschaft m.b.H., 1934, 17, part 2, 76. (6) Die Messung von Hörschwellen mit dem Überlagerungssumme, *Zeits. Hals-Nasen-Ohrenheilk.*, 1930, 27, 418.
- Meyer, E., and Cremer, L. Über die Hörsamkeit holzausbekleideter Räume, *Zeits. techn. Physik*, 1933, 14, 500.
- Meyer, E., and Keidel, L. Röhrenvoltmeter mit logarithmischer Anzeige und seine Anwendungen in der Akustik, *Elektr. Nachr. Techn.*, 1935, 12, 37.
- Meyer, E., and Waetzmann, E. Über den Grad der Dämpfung der Ohrresonatoren, *Naturwissenschaften*, 1925, 13, 268-271.
- Meyer, Max F. (1) Zur Theorie der Differenzöne und der Gehörsempfindungen überhaupt, *Zeits. Psychol.*, 1898, 16, 1-34. (2) Ueber die Intensität der Einzelöne zusammen gesetzter Klänge, *Zeits. Psychol.*, 1898, 17, 1-14.
- Micksch, Karl. *Taschenbuch der Kette und Klebstoffe*, 2d ed., Stuttgart, 1941.
- Moe, C. R. An experimental study of subjective tones produced within the human ear, *J. Acoust. Soc. Amer.*, 1942, 14, 159-166.
- Müller, Johannes, and Pouillet, Claude S. M. *Lehrbuch der Physik*, 11th ed., vol. 1, Brunswick, Germany, Vieweg-Verlag, 1934.
- Nernst, Walther. (1) *Theoretische Chemie vom Standpunkte der Avogadro'schen Regel und der Thermodynamik*, Stuttgart, Ferd. Enke Verlag, 1898, Eng. trans. by H. T. Tizard, London, Macmillan & Co., Ltd., 1916. (2) Zur Theorie des elektrischen Reizes, *Pflüg. Arch. ges. Physiol.*, 1908, 122, 275.
- Nernst, W., and Reisenfeld, E. H. Ueber elektrolytische Erscheinungen an der Grenzfläche zweier Lösungsmittel, *Ann. Physik*, 1902, 8, 600.
- Neubert, K. Die Basilarmembran des Menschen und ihr Verankerungssystem (Ein morphologischer Beitrag zur Theorie des Hörens), *Zeits. Anat. Entwickl.*, 1950, 114, 539-588.
- Ohm, G. S. (1) Ueber die Definition des Tons, nebst daran geknüpfter Theorie der Sirene und ähnlicher tonbildender Vorrichtungen, *Ann. Physik*, 1843, 59, 497-565. (2) Noch ein Paar Worte über die Definition des Tons, *Ann. Physik*, 1844, 62, 1-17.
- Olson, H. F. *Dynamic Analogies*, Princeton, N.J., D. Van Nostrand Company, Inc., 1943, 94-96.
- Olson, F., and Kreuzer, B. The reverberation time bridge, *J. Acoust. Soc. Amer.*, 1930, 2, 78-82.
- Opheim, O., and Flottorp, G. The aural harmonics in normal and pathological hearing: A new method of demonstration of the recruitment phenomena, *Acta Oto-laryngol.*, 1955, 45, 513-531.

- Pattie, F. A., Jr. A further experiment on auditory fatigue, *Brit. J. Psychol.*, 1929, 20, 38-42.
- Pauli, Richard. (1) *Psychologisches Praktikum*, 3d ed., Jena, Fischer Verlag, 1923. (2) *Über psychische Gesetzmässigkeiten*, Jena, Fischer Verlag, 1920.
- Penfield, Wilder, and Boldrey, E. Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation, *Brain*, 1937, 60, 389-443.
- Penfield, Wilder, and Rasmussen, T. *The Cerebral Cortex in Man*, New York, The Macmillan Company, 1950, 25.
- Peterson, L. C., and Bogert, B. P. A dynamical theory of the cochlea, *J. Acoust. Soc. Amer.*, 1950, 22, 369-381.
- Planck, M. Ueber die Potentialdifferenz zwischen zwei verdünnten Lösungen binärer Electrolyte, *Ann. Physik*, 1890, 40, 561.
- Pohl, R. W. *Mechanik und Akustik*, Berlin, Springer-Verlag, 1930.
- Politzer, Adam. (1) Untersuchungen über die Schallfortpflanzung und Schalleitung im Gehörorgane (im gesunden und kranken Zustande), *Arch. Ohrenheilk.*, 1864, 1, 59-73. (2) *Wandtafeln zur Anatomie des Gehörganges*, 1873. (3) *Zergliederung des menschlichen Gehörorganes*, Stuttgart, Ferd. Enke Verlag, 1889.
- Pollack, I. The atonal interval, *J. Acoust. Soc. Amer.*, 1948, 20, 146-149.
- Pritchard, U. The cochlea of the *Ornithorhynchus platypus* compared with that of ordinary mammals and of birds, *Trans. Roy. Soc. London*, 1881, 172, part II, 267.
- Procopiu, S. Sur la force électromotrice produite par le déplacement relatif d'une électrode et d'un électrolyte, *J. Chim. phys.*, 1921, 19, 121.
- Quincke, G. Ueber die Fortführung materieller Theilchen durch strömende Elektrizität, *Ann. Phys. Chemie*, 1861, 113, 513.
- Rabinovich, A. V. Effect of distance in the broadcasting studio, *J. Acoust. Soc. Amer.*, 1935, 7, 199.
- Ranke, Otto F. (1) *Die Gleichrichter-Resonanztheorie*, Munich, J. Lehmann, 1931. (2) Physiologie der Schnecke und des Cortischen Organs, *Ergebn. Physiol.*, 1935, 37, 12-81. (3) Das Massenverhältnis zwischen Membran und Flüssigkeit im Innenohr, *Akust. Zeits.*, 1942, 7, 1-11. (4) Theory of operation of the cochlea: Contribution to the hydrodynamics of the cochlea, *J. Acoust. Soc. Amer.*, 1950, 22, 772-777. (5) Hydrodynamik der Schneckenflüssigkeit, *Zeits. Biol.*, 1950, 103, 409. (6) *Physiologie des Gehörs*, Berlin, Springer-Verlag, 1953.
- Ranvier, L. *Traité technique d'histologie*, Paris, F. Savey.
- Rayleigh, Lord. *Theory of Sound*, London, Macmillan & Co., Ltd., 1877, reprinted 1929.
- Rejtö, A. Beiträge zur Physiologie der Knochenleitung, *Verh. Deutsche. otol. Ges.*, 1914, 23d Versammlung, 268-285. Jena, Fischer Verlag, 1914.
- Renaut, J. *Traité d'histologie pratique*, II, Paris, Rueff, 1893-1899.
- Rettinger, M. Note on reverberation characteristics, *J. Acoust. Soc. Amer.*, 1934, 6, 51.
- Retzius, G. *Das Gehörorgan der Wirbeltiere*, vol. I, *Gehörorgan der Fische und Amphibien*; II, *Das Gehörorgan der Reptilien, der Vögel, und der Säugetiere*, Stockholm, Samson and Wallin, 1881, 1884.
- Reynolds, O. On the refraction of sound by the atmosphere, *Proc. Roy. Soc. London*, 1874, 22, 531-548.
- Riegger, H. Objective Klangaufzeichnung mittels des Kondensatormikrophons, quoted in F. Trendelenburg, *Wiss. Veröffentl. Siemens-Konzern*, 1924, 3, 43.
- Riesz, R. R. (1) Differential intensity sensitivity of the ear for pure tones, *Phys. Rev.*, 1928, 31, 867. (2) The relationship between loudness and the minimum perceptible increment of intensity, *J. Acoust. Soc. Amer.*, 1933, 4, 211-216.
- Roaf, H. E. The analysis of sound waves by the cochlea, *Phil. Mag.*, 1922, 43, 349-354.
- Roberts, W. H. Discrimination by sense of touch, *J. Franklin Inst.*, 1932, 213, 286-312.
- Robinson, C. A direct-reading frequency meter for telephone currents, *Post Office elect. Engng. J.*, 1923, 16, 171.

- Rohracher, H. *Mechanische Mikroschwingungen des menschlichen Körpers*, Vienna, Urban & Schwarzenberg, 1949.
- Roux, W. *Gesamte Abhandlungen über die Entwicklungsmechanik der Organismen*, Leipzig, W. Engelmann, 1895.
- Ruch, T. C. (1) Sensory mechanisms, in S. S. Stevens' *Handbook of Experimental Psychology*, New York, John Wiley & Sons, Inc., 1951, 121-153. (2) Somatic sensations, in J. Fulton (ed.), *Howell's Textbook of Physiology*, 17th ed., Philadelphia, W. B. Saunders Company, fig. 199, p. 325. (3) Audition and the auditory pathways, *ibid.*, pp. 399-423.
- Runge, C., and Emde, F. *Rechnungsformulare*, Brunswick, Germany, Vieweg-Verlag, 1913.
- Rutherford, W. The sense of hearing, *J. of Anat. Physiol.*, 1886, 21, 166-168.
- Sabine, W. C. *Collected Papers on Acoustics*, Cambridge, Mass., Harvard University Press, 1922.
- Sacia, C. F. Photomechanical wave analyser applied to inharmonic analysis, *J. Opt. Soc. Amer.*, 1924, 9, 487.
- Saul, L. J., and Davis, H. (1) Electrical phenomena of the auditory mechanism, *Trans. Amer. Otol. Soc.*, 1932, 22, 137-145. (2) Action currents in the central nervous system, *Arch. Neurol. Psychiat.* 1932, 28, 1104.
- Schäfer, K. L., and Giesswein, M. Physiologie des äusseren und mittleren Ohres und der Schnecke, in Alfred Denker and O. Kahler's *Handbuch der Hals- Nasen- Ohrenheilkunde*, vol. 6, *Die Krankheiten des Gehörorgans*, part 1, Berlin, Springer-Verlag, 1926, 389-518.
- Schelhammer, Gunther C. *De auditu*, liber unus, Lugduni Batavorum, 1684.
- Schmiescheck, U. Experimenteller Nachweis der Vibrationsbewegungen physikalischer Moleküle, *Zeits. tech. Physik*, 1934, 15, 178.
- Schouten, J. F. Synthetischer Schall, *Philips Tech. Rundschau*, 1939, 4, 176-183.
- Schuster, K. Messung von akustischen Impedanzen durch Vergleich, *Elektr. Nachr. Techn.*, 1936, 13, 164.
- Schuster, K., and Waetzmänn, E. Über den Nachhall in geschlossenen Räumen, *Ann. Physik*, 1929, 1, 671.
- Schwarz. Gesichtspunkte für den Bau von Knochentelefonen, *Zeits. Hals- Nasen- Ohrenheilk.*, 1930, 27, 434.
- Sell, H. (1) Drei Demonstrationsversuche auf dem Gebiete der Schwingungstechnik, *Zeits. techn. Physik*, 1927, 8, 226. (2) Eine neue kapazitive Methode zur Umwandlung mechanischer Schwingungen in elektrische und umgekehrt, *Zeits. techn. Physik*, 1937, 18, 3.
- Shambaugh, G. E. (1) Die Membrana tectoria und die Theorie der Tonempfindung, *Zeits. Ohrenheilk.*, 1909, 59, 159-168. (2) Das Verhältnis zwischen der Membrana tectoria und dem Cortischen Organ, *Zeits. Ohrenheilk.*, 1910-1911, 62, 235-240.
- Sherrington, Charles. *The Integrative Action of the Nervous System*, New Haven, Conn., Yale University Press, 1947.
- Sivian, L. J. Acoustic impedance of small orifices, *J. Acoust. Soc. Amer.*, 1935, 7, 94.
- Sivian, L. J., and White, S. D. On minimum audible sound fields, *J. Acoust. Soc. Amer.*, 1933, 4, 288-321.
- Skramlik, Emil v. *Psychophysiologie der Tastsinn*, Leipzig, Akademische Verlagsgesellschaft m.b.H., 1937 (*Arch. ges. Psychol.*, 4th Ergänzb.).
- Skudrzyk, E. *Die Grundlagen der Akustik*, Vienna, Springer-Verlag, 1954.
- Soest, J. L. van, and Groot, P. D. Stereoacoustische Geluidsbeelden en kleinst Waarneembare Tijdsverschillen, *Physica*, 1929, 9, 111.
- Steinberg, I., and Snow, W. Auditory perspective: Physical factors, *Electronic Engng.*, 1934, 53, 12.
- Steinberg, J. C. Symposium: Neural mechanism of hearing: Hearing aids for "nerve deafness," *Laryngoscope*, 1937, 47, 603-611.
- Steinberg, J. C., and Gardner, M. B. The dependence of hearing impairment on sound intensity, *J. Acoust. Soc. Amer.* 1937, 9, 11-23.
- Stern, W. L. Psychische Präsenzzeit, *Zeits. Psychol.*, 1897, 13, 325-348.

- Steudel, U. Ueber Empfindung und Messung der Lautstärke, *Hoch. Elektroakust.*, 1933, 41, 116-128.
- Stevens, S. S. The relation of pitch to intensity, *J. Acoust. Soc. Amer.*, 1935, 6, 150.
- Stevens, S. S., Carton, A. S., and Shickman, G. M. A scale of apparent intensity of electric shock, *J. exp. Psychol.* 1958, 56, 328-338.
- Stevens, S. S., and Davis, H. *Hearing, Its Psychology and Physiology*, New York, John Wiley & Sons, Inc., 1938, 345.
- Stevens, S. S., Davis, H., and Lurie, M. H. The localization of pitch perception on the basilar membrane, *J. gen. Psychol.*, 1935, 13, 297-315.
- Stevens, S. S., and Newman, E. B. The localization of pure tones, *Proc. Nat. Acad. Sci., U.S.*, 1934, 20, 593-596.
- Stewart, G. W. Direct absolute measurement of acoustic impedance, *Phys. Rev.*, 1926, 28, 1038.
- Stewart, George W., and Lindsay, R. B. *Acoustics*, Princeton, N.J., D. Van Nostrand Company, Inc., 1930.
- Strutt, M. J. O. (1) Raumakustik, in W. Wien and F. Harms, *Handbuch der experimentellen Physik*, Leipzig, Akademische Verlagsgesellschaft m.b.H., 1934, part 2, 443-512. (2) Strahlung von Antennen unter dem Einfluss der Erdbodeneigenschaften, *Ann. Physik*, 1929, 1, 721. (3) *Ibid.*, 751. (4) Reflexionsmessungen mit sehr kurzen elektrischen und mit akustischen Wellen, *Elektr. Nachr. Techn.*, 1930, 7, 65. (5) On the acoustics of large rooms, *Phil. Mag.*, 1929, 8, 236. (6) Über eine vollautomatische Nachhallmessvorrichtung, *Elektr. Nachr. Techn.*, 1930, 7, 280. (7) On the amplitude of driven loudspeaker cones, *Exp. Wireless*, 1931, 8, 238. (8) Strahlung von Antennen unter dem Einfluss der Erdbodeneigenschaften, *Ann. Physik*, 1931, 9, 67.
- Stuhlman, Otto, Jr. The non-linear transmission characteristics of the auditory ossicles, *J. Acoust. Soc. Amer.*, 1937, 9, 119-128.
- Stumpf, Carl. (1) *Tonpsychologie*, II, Leipzig, S. Hirzel Verlag, 1883-1890. (2) Ueber die Ermittlung von Obertönen, *Ann. Phys. Chemie*, 1896, 57, 660-681. (3) Beobachtung über Kombinationstöne, *Zeits. Psychol.*, 1910, 55, 1-144. (4) *Die Sprachlaute*, Berlin, Springer-Verlag, 1926.
- Tasaki, I. Nerve impulses in individual auditory nerve fibers of guinea pig, *J. Neurophysiol.*, 1954, 17, 97.
- Tasaki, I., Davis, H., and Legoux, J. P. The space-time pattern of the cochlear microphonics (guinea pig), as recorded by differential electrodes, *J. Acoust. Soc. Amer.*, 1952, 24, 502-519.
- Taylor, S. On variations of pitch in beats, *Phil. Mag.*, 1872, 44, 56.
- Thévenin, L. Sur un nouveau théorème d'électricité dynamique, *Compt. rend. Acad. Sci., Paris*, 1883, 97, 159.
- Timoshenko, S. *Schwingungsprobleme der Technik*, Berlin, Springer-Verlag, 1932.
- Tischner, H. Über die Fortpflanzung des Schalles in Röhren, *Elektr. Nachr. Techn.*, 1930, 7, 192.
- Todd, B., and Bowman, W. *The Physiological Anatomy and Physiology of Man*, London, Parker, 1856.
- Tower, O. F. Ueber Potentialdifferenzen an den Berührungsflächen verdünnter Lösungen, *Zeits. Phys. Chemie*, 1896, 20, 198.
- Trautwein, F. Toneinsatz und elektrische Musik, *Zeits. techn. Physik*, 1932, 13, 244.
- Trendelenburg, F. (1) Objektive Klangaufzeichnung mittels des Kondensatormikrophons, *Wiss. Veröfentl. Siemens-Konzern*, 1924, 3, 43. (2) Klänge und Geräusche, Berlin, Springer-Verlag, 1935. (3) Frequenz und Dekrement der Eigenschwingungen der Mundhöhle bei Vokalstellungen, *Sitzungsber. Akad. Wiss., Berlin, phys.-math. Kl.*, 1936, 308-321.
- Trendelenburg, W., and Schütz, E. Ueber den Muskelton, *Zeits. Biol.*, 1929, 89, 41.
- Tröger, J. Die Schallaufnahme durch das äussere Ohr, *Phys. Zeits.*, 1930, 31, 26-47.
- Tschachotin, S. Eine Mikrooperationsvorrichtung, *Zeits. wiss. Mikr.*, 1912, 29, 188.
- Tschermak-Seysenegg, A. v. *Einführung in die physiologische Optik*, 1942; *Introduction to Physiological Optics*, Trans. by Paul Boeder, Springfield, Ill., Charles C Thomas, Publisher, 1952.
- Vierordt, K. *Der Zeitsinn nach Versuchen*, Tübingen, H. Laupp, 1868.

- Voigt, W. *Lehrbuch der Kristallphysik*, Leipzig, Teubner Verlagsgesellschaft, 1910.
- Vrijdaghs, J. J. H. A new property of the ear? *Exp. Wireless*, 1934, 11, 196.
- Waar, A. G. H. Mikroskopische Wahrnehmungen der Funktion der Mittelohrmuskeln beim Menschen, *Acta Oto-laryngol.*, 1923, 5, 335-358.
- Waetzmann, E. (1) *Die Resonanztheorie des Hörens*, Brunswick, Germany, Vieweg-Verlag, 1912. (2) Die Entstehungsweise von Kombinationstönen im Mikrophon-Telephonkreis, *Ann. Physik*, 1913, 42, 730. (3) Die Resonanztheorie des Hörens, *Naturwissenschaften*, 1922, 10, 542-551. (4) Moderne Probleme der Akustik, *Phys. Zeits.*, 1925, 26, 740. (5) Ton, Klang und sekundäre Klangercheinungen, in A. Bethe (ed.), *Handbuch der normalen und pathologischen Physiologie*, 11, *Receptionsorgane I*, Berlin, Springer-Verlag, 1926, 579. (6) Ein erb-biologisches Problem am menschlichen Gehörorgan, *Nachr. Ges. Wiss. Göttingen, math.-phys. Kl., Biol.*, 1935, 1, 157-161. (7) Über die Empfindlichkeit des menschlichen Ohres, in *Festschrift der Technischen Hochschule Breslau zur Feier ihres 25 jährigen Bestehens 1910-1935*, 1935, 478. (8) In Müller, Johannes, and Pouillet, C. S. M., *Lehrbuch der Physik*, 11th ed., vol. 1, Brunswick, Germany, Vieweg-Verlag, 1934. (9) Über Symmetrie- und Erblchkeitsfragen am menschlichen Gehörorgan, *Zeits. techn. Physik*, 1936, 17, 549-553; and *Akust. Zeits.*, 1936, 1, 155-159. (10) Absorptionsmessungen am Trommelfell mit der Schusterschen Brücke, *Akust. Zeits.*, 1938, 3, 1.
- Waetzmann, E., and Heisig, H. Untersuchungen über akustische Schwellenwerte, *Ann. Physik*, 1931, 9, 921; also vol. 10, 846.
- Waetzmann, E., and Keibs, L. (1) Theoretischer und experimenteller Vergleich von Hörschwellenmessung, *Akust. Zeits.*, 1936, 1, 3-12. (2) Hörschwellenbestimmungen mit dem Thermophon und Messungen am Trommelfell, *Ann. Physik*, 1936, 26, 141-144.
- Waetzmann, E., and Noether, F. Über akustische Filter, *Ann. Physik*, 1932, 13, 212.
- Waetzmann, E., and Schuster, K. Raum- und Bauakustik; Berechnung der Nachhalldauer, in Johannes Müller and C. S. M. Pouillet's *Lehrbuch der Physik, Akustikband*, Brunswick, Germany, Vieweg-Verlag, 1929.
- Wagner, K. W. (1) Zur Geschichte der elektrischen Siebketten, *Arch. Elektrotechnik*, 1927, 18, 78. (2) Kettenleiter und Wellensiebe, *Elektr. Nachr. Techn.*, 1928, 5, 1. (3) Ein neues elektrisches Sprechgerät zur Nachbildung der menschlichen Vokale, *Abhandl. Akad. Wiss., Berlin, phys.-math. Kl.*, 1936.
- Watson, N. A. Limits of audition for bone conduction, *J. Acoust. Soc. Amer.*, 1938, 9, 294.
- Watson, N. A., and Knudsen, V. O. Ear defenders, *J. Acoust. Soc. Amer.*, 1944, 15, 153.
- Wegel, R. L., and Lane, C. E. The auditory masking of one pure tone by another and its probable relation to the dynamics of the inner ear, *Phys. Rev.*, 1924, 23, 266-285.
- Wente, E. C. The effect of the acoustics of an auditorium on the interpretation of speech, *Amer. Architect.*, August 20, 1928, 134.
- Wente, E. C., and Bedell, E. H. A chronographic method of measuring reverberation time, *J. Acoust. Soc. Amer.*, 1930, 1, 422.
- Werner, C. F. *Das Labyrinth*, Stuttgart, Georg Thieme Verlag, 1940.
- West, W. (1) Measurements of the acoustical impedance of human ears, *Post Office elect. Engng. J.*, 1929, 20, 293. (2) An artificial ear, *Post Office elect. Engng. J.*, 1930, 22, 260. (3) The pressures in the diaphragm of a condenser transmitter in a simple sound field, *J. Inst. Elec. Engr.*, 1930, 68, 441.
- Wever, E. G. (1) Beats and related phenomena resulting from the simultaneous sounding of two tones, *Psychol. Rev.*, 1929, 36, 402-418, 512-523. (2) *Theory of Hearing*, New York, John Wiley & Sons, Inc., 1949, fig. 30, p. 149.
- Wever, E. G., and Bray, C. W. (1) Action currents in the auditory nerve in response to acoustical stimulation, *Proc. Nat. Acad. Sci., U.S.*, 1930, 16, 344-350. (2) Present possibilities for auditory theory, *Psychol. Rev.*, 1930, 37, 365-380. (3) The nature of acoustical response: The relation between the sound frequency and frequency of impulses in the auditory nerve, *J. exper. Psychol.*, 1930, 13, 373-387.
- Wever, E. G., Bray, C. W., and Lawrence, M. (1) The locus of distortion in the

- ear, *J. Acoust. Soc. Amer.*, 1940, 11, 427-433. (2) The nature of cochlear activity after death, *Ann. of Otol. Rhinol. Laryngol.*, 1941, 50, 317-329.
- Wever, E. G., and Lawrence, M. (1) The place principle in auditory theory, *Proc. Nat. Acad. Sci., U.S.*, 1952, 38, 133-138. (2) Sound conduction in the cochlea, *Ann. of Otol. Rhinol. Laryngol.*, 1952, 61, 824-834. (3) *Physiological Acoustics*, Princeton, N.J., Princeton University Press, 1954.
- Wever, E. G., Lawrence, M., and Békésy, G. v. A note on recent developments in auditory theory, *Proc. Nat. Acad. Sci., U.S.*, 1954, 40, 508-512.
- Wever, E. G., Lawrence, M., Hemphill, R. W., and Straut, C. B. Effects of oxygen deprivation upon the cochlear potentials, *Amer. J. Physiol.*, 1949, 159, 199-208.
- Wiechert, E. Eine neue Methode zur Messung des Erdableitungswiderstandes von Blitzableitern, *Elektrotech. Zeits.*, 1893, 14, 726.
- Wien, M. Ein Bedenken gegen die Helmholtzsche Resonanztheorie des Hörens, *Festschrift für Adolph Wüllner*, Leipzig, Teubner Verlagsgesellschaft, 1905, 28-35.
- Wiener, F. M. On the diffraction of a progressive sound wave by the human head, *J. Acoust. Soc. Amer.*, 1947, 19, 143-146.
- Wiener, F. M., and Ross, D. A. The pressure distribution in the auditory canal in a progressive sound field. *J. Acoust. Soc. Amer.*, 1946, 18, 401-408.
- Wiener, O. Darstellung gekrümmter Lichtstrahlen und Verwerthung derselben zur Untersuchung von Diffusion und Wärmeleitung, *Ann. Physik*, 1893, 49, 105.
- Wilkinson, G. (1) The mechanism of the cochlea, *Nature, London*, 1922, 110, 560. (2) A note on the resonating system in the cochlea with demonstration of a model illustrating the action of a hitherto neglected factor. *J. Physiol.*, 1922, 56, ii-iv.
- Wilkinson, G., and Gray, A. A. *The Mechanism of the Cochlea*, London, Macmillan & Co., Ltd., 1924.
- Wilska, A. Eine Methode zur Bestimmung der Hörschwellenamplituden des Trommelfells bei verschiedenen Frequenzen, *Skand. Arch. Physiol.*, 1935, 72, 161-165.
- Wittmaack, K. Ueber experimentelle Schallschädigung mit besonderer Berücksichtigung der Körperleitungsschädigung, *Beitr. Anat., etc. Ohr.*, 1917, 9, 1-37.
- Wrightson, Thomas. *The Analytical Mechanism of the Internal Ear*, London, Macmillan & Co., Ltd., 1918.
- Zimmermann, K. W. Mechanism of excitation of hairs of auditory cells, *Schweiz. med. Wochenschr.*, 1926, 56, 566.
- Zoller, K. Die Bewegung einer starren Kugel infolge einer Druckwelle, *Akust. Zeits.*, 1943, 8, 213.
- Zurmühl, G. Abhängigkeit der Tonhöhenempfindung von der Lautstärke und ihre Beziehung zur Helmholtzschen Resonanztheorie des Hörens, *Zeits. Sinnesphysiol.*, 1930, Abt. II, 61, 40.
- Zwislocki, J. (1) Theorie der Schneckenmechanik, *Acta Oto-laryngol.*, 1948, suppl. 72. (2) Theory of the acoustical action of the cochlea, *J. Acoust. Soc. Amer.*, 1950, 22, 778. (3) Wave motion in the cochlea caused by bone conduction, *J. Acoust. Soc. Amer.*, 1953, 25, 986-989.

INDEX

- Abnormalities of hearing, 88, 624-625
- Absolute loudness, 215
- Absorbent surfaces, effects of, 392-399, 525
- Absorption of sound, by audience, 394, 398-399
 - by padded frame, 389
 - by walls of room, 381-383
- Acoustic impedance (*see* Impedance)
- Acoustic roughness, 344-353
- Acoustics, of rooms, 302, 321-322, 331-332, 369-399
 - of tents, 386-389
- Adaptation for skin, 559, 586
 - (*See also* Fatigue)
- Adhesive tape, effect on skin sensitivity, 617-618
- Adhesives, 21, 447
- Adrian, E. D., 641, 685, 715
- Air conduction, cancellation by bone conduction, 128
 - (*See also* Threshold)
- Air flow from sound source, 307
- Albert, K., 556, 715
- Alcohol, effect on sensitivity, 207
- Alexander, G., 715
- Alligator, organ of Corti, 486
- Alternating potentials of cochlea (*see* Cochlear microphonics)
- Amplifier for d-c pulses, 649
- Amplitude, mechanical, determination, 49-57
- Analogies, electrical, 19
- Analysis (*see* Frequency analysis)
- Anatomical techniques, 12-13, 17-32, 34, 49
- Anatomy of ear, 11-18
 - (*See also* Anatomical techniques)
- Andrejew, N., 113, 715
- Anesthesia, effect of, on cochlear potentials, 485, 673
 - on perilymph pressure, 688
 - on skin sensitivity, 600
- Animals, sensitivity to own vocalizations, 181
- Ankylosis of incudomalleolar joint, 115
- Anoxia, effect on potentials of cochlea, 640-642, 645, 654, 677, 682, 689, 700
- Anvil, 11
 - (*See also* Ossicles)
- Area of apprehension, 374
- Areal distribution of vibratory sensations, 591, 598-599, 613, 619
 - effects of fatigue on, 627
- Areal stimulation of skin, 617-618, 622, 625
- Armrests for dissection, 23-24
- Artifacts, in cochlear potential measurements, 676-678
 - in histology, 17-18
 - in middle-ear measurements, 96, 98-100
- Artificial stapes, 427, 482
- Atonal interval, 622-624
- Attack in speech and music, 393
- Attention, 291, 371
 - (*See also* Distraction)
- Attenuation, across head, 86-87, 163, 174-176, 415
 - voltage (*see* Voltage attenuation)
 - of waves by absorbent surfaces, 392-399, 525
- Attenuator, cotton-plug type, 63
- Attitude, spatial, 375
- Attwood, S. S., 662, 715
- Audience as absorber of sound, 394, 398-399
- Audiograms, disturbed, 91
 - normal, 84-85
 - pathological, 88-90
 - (*See also* Threshold)
- Audiometer, 81-91
- Audiometry methods, 81-91, 139, 163
- Auditory beats (*see* Beats)
- Auditory echoes, 557-558, 632
- Auditory nerve, 16
- Auditory ossicles (*see* Ossicles)
- Auditory space, center, 287
- Auditory and tactual intensities compared, 249

- Auditory theory, 539-546
 forms of simplification, 443-446
 (See also Duplexity theory of hearing;
 Resonance theories; Standing-
 wave theory; Traveling-wave
 theory)
 Auditory tube, 11
 click produced by, 314-315
 Automatic techniques, 6-7
 anatomical, 34, 49
 recording, 68
- Backhaus, H., 53, 393, 549, 555, 578,
 603, 715
 Ballantine, S., 267-268, 715
 Bárány, E., 102, 129, 150, 164, 166,
 177, 181, 201, 485, 715
 Bárány, R., 108, 715
 Barkhausen, H., 378, 415, 715
 Barlow, H. B., 612, 715
 Bartlett, F. C., 277, 715
 Basilar membrane, 12
 response characteristics, 104, 315-318
 curve of excitation, 256
 form of motion, 229, 232, 480, 496
 for clicks, 311-312
 patterns of response along, 172-173,
 255, 354, 366-367, 403-484,
 540-541
 by bone conduction, 127
 phase of responses, 460-463
 selectivity, 446-449, 454-455
 tension, 464-465, 471-473
 (See also Cochlea, as frequency
 analyzer)
 structural characteristics, 404
 coupling with fluids, 495
 damping, 229, 232, 254-255, 404,
 410-416, 458-460
 effects of static pressure on, 472-476
 elasticity, 408, 472-476, 540-542
 form, 28-29
 loading, 445-446, 496
 reference points on, 28
 relation to stapes, 256-257
 width, 405, 473
- Bat, organ of Corti, 487
 Beating tones, localization, 299-300
 Beats, auditory, 229-235, 574-578, 587-
 590
 binaural, 349-350
 effect on reverberation curves, 385
 fatigue produced by, 353, 536-537
 method of best beats, 87, 176, 333,
 336, 577-590
 roughness, 345-352
 vibratory, on skin, 574-575, 578-590
- Beatty, R. T., 535, 715
 Bedell, E. H., 369, 727
 Beljers, H. J., 348, 715
 Benecke, H., 332, 715
 Berendes, Z., 474, 715
 Berger, R., 495, 715
 Bernamont, J., 55, 715
 Best-beats method, 87, 176, 333, 336,
 557-590
 Binaural beats, 349
 Binaural disparity, in intensity, 297-301
 in time, 273-278, 282-287
 time-intensity relations, 300-301
 (See also Sound images, location;
 Sound location)
 Binaural hearing, 566-568
 Binaural images, 297
 Binaural summation, 219, 223-226, 235
 Birds, hearing of, 564
 structure of ear, 486, 501
 Birkhoff, G., 511, 716
 Biting board, 72
 Bleeker, J. D., 695, 716
 Blind spot of retina, effect of illuminat-
 ing, 538
 Blood pulsations, effect on hearing, 487
 Böhme, H., 158, 716
 Bogert, B. P., 526, 666, 716, 724
 Boldrey, E., 565, 724
 Bolton, T. L., 716
 Bone conduction, 127-203
 action of mandible in, 129, 143-144
 cancellation by air conduction, 128
 compression of cochlea in, 145-147
 from earphones, 225
 effects of mastoid operation on, 162-
 163
 form of vibrations in, 144-145
 minimizing, 199-200
 theory, 140, 143-145
 Bone-conduction receivers, 133-134,
 150-151, 158-159
 Bone-conduction tests, 129, 131-133,
 148, 163
 Bone-conduction thresholds, 131-136,
 148, 160-162, 172-173, 191-192
 Bone dust, 22
 Bone forceps, 22
 Bonnier, P., 355, 366, 368, 405, 716
 Boundaries, methodological, 9-10
 Bowman, W., 726
 Brain, sensory areas, 564-566
 Braunmühl, H. J. von, 716
 Bray, C. W., 577, 641, 684, 685, 727
 Breakpoint, 278
 Brecher, G. A., 258, 260, 261, 716
 Breisig, F., 355, 716
 Breuer, C., 447, 716

- Breuer, J., 703, 716
 Brillouin, L., 55, 716
 Brinitzer, W., 716
 Broom, R., 181, 716
 Brownian movements, 486
 Bruine-Altes, J. C. de, 716
 Bubbles in cochlea, removal, 426-427
 Buchthal, F., 716
 Budde, E., 419, 716
 Build-up of vibratory sensation in time, 559, 598
 Bulla, auditory, function of, 199-200
 Burlet, H. M. de, 716
 Burning sensation from tonal stimulation, 263
 (See also Pain; Pricking in ear; Prickle)
 Burr, H. S., 637, 716
 Bush, V., 75, 716
 Byford, G. H., 719
- Calf, cochlea, 507
 eardrum, 194
 Camera acustica (of Ewald), 428
 Camera lucida, 29
 Canalis facialis, 430-431
 Capacity of cochlear membranes, 689-690
 (See also Impedance, electrical)
 Capillaries, impedance, 138
 Capillary circulation in cochlea, 673
 Capillary forces in dissection, 26
 Carson, J. R., 716
 Carton, A. S., 619, 726
 Catenary hypothesis, 95-96
 Cavities, method of studying, 22
 Cements, 21, 447
 Center of head, determination, 286
 Central nervous system in directional hearing, 272
 Chambers, R., 716
 Chapin, E. K., 716
 Chicken, anatomy of ear, 196-198, 504-505
 sensitivity to own vocalizations, 183-184
 sound analysis by, 504-506
 Chisel, use in anatomy, 22
 Chocholle, R., 577, 716, 722
 Cilia of hair cells, 14
 Circulatory variations, effect on hearing, 487
 Clicks, action on eardrum, 314-315, 319
 localization, 276
 produced by swallowing, 314
 stimulation of skin by, 621-622, 629-631
 (See also Pulses)
- Clinical tests of hearing, 88, 135, 148, 163
 (See also Audiometry)
 Cocaine, effect on sensitivity, 207
 Cochlea, 11
 bubble removal, 426-427
 capillary circulation in, 673
 compression in bone conduction, 145-147
 decay time for, 459-460
 eddies (see Eddies)
 effect of opening, 483
 electrical energy source in, 635-637, 642-647, 654
 electrical insulation in, 661, 686-687, 689, 694
 electrical resistance, 654-672
 electroanatomy, 653-672, 685-686
 energy balance in, 636-647
 energy flow in, 512, 526
 evolution, 249, 485-487, 500-510
 fluid columns, 427, 444, 458
 fluid displacement, 202
 fluid pathways, 104, 106
 form, 200, 499-500
 as frequency analyzer, 60, 404, 410-416, 428-429, 446-449, 454-455, 500-510, 535-539
 grounding pathway, 660-661
 hydrodynamic theories, 444
 hypertension, 587
 insulation in, 666-672
 length in various animals, 503-508
 linearity of responses in, 481
 localization of response in, 440-443, 463, 505-509
 (See also Basilar membrane, patterns of response along)
 maximum tolerable current, 656-657
 models (see Cochlear models)
 nonlinearity (see Distortion)
 number of turns, 425
 numerical values for, 403
 opening, 25-29, 32, 425-427, 429, 446-452
 pathological conditions in, 533-534
 polarization in, 656-657
 rectification in, 361
 shock waves in, 456-457
 spiral diagrams, 503-508
 structure of cross section, 443
 traveling waves in, 425, 461, 494, 512
 visual observation of movements in, 441-443, 446-455, 459-460
 method of preparing for, 446-453
 voltage attenuation in, 661, 664-666
 voltage pattern, 653-672, 685-686

- Cochlea, wave travel in, 510-512, 525-526
 paradoxical, 510-512, 532-533
(See also Standing waves in cochlea)
- Cochlear duct, 438, 452
- Cochlear fluid, distribution of potentials in, 694-695
 mobility, 434-435
(See also Endolymph; Perilymph)
- Cochlear hypertension, 587
- Cochlear injury, 440
- Cochlear microphonics, 635-710
 distortion in, 577
 effect on, of anoxia, 640-641
 of direct currents, 656-657
 energy source for, 635-639, 642-644
 with perforating electrode, 688-692
 place of origin, 635-636, 684-710
 polarity, 707-709
 for study of cochlear patterns, 493-494
 types, 641
 first-order, 686
 second-order, 696, 701
 with vibrating electrode, 636, 672-684, 697, 702-703
 effect of direction of vibration, 682-684
 relation of displacement and velocity, 680-681
- Cochlear models, eddies in, 420-423, 445
 electrical, 661-664, 690-695
 hydraulic, using skin as receptor, 445, 551-634
 mechanical, dimensional type, 405-410, 437-445, 510-512, 540-544
 pendulum type, 519, 526-534, 542-543
 tuned-reed type, 515-524, 545, 548-550
 using skin as receptor, 545-547, 551
 traveling waves in, 517-524
 vibratory patterns in, 419-423
- Cochlear partition, 11, 466
 conductivity, 661-664
 damping, 644
 effect of mechanical shock on, 642
 form of vibration, 461-463, 493-496
 maximum amplitude of response to tones, 440-443, 455, 505-509
 phase relations along, 461, 466
 resonance, 454-455, 460-462, 494, 504-510
 spiral diagrams, 503-508
 static deformation, 644-645
 stiffness, 467-480, 483, 510
(See also Basilar membrane)
- Cochlear patterns, 403-484
(See also Cochlear partition, form of vibration)
- Cochlear potentials, 635-710
 effect of anoxia on, 640-642, 645, 654, 677, 682, 689, 700
 energy source for, 635-639, 642-644
 phase relations in, 689-690
 types, 641
(See also Cochlear microphonics; Direct potentials of cochlea; Nerve potentials)
- Cochlear resonators, characteristics, 444
 effect of phase shift on, 411-413
 onset time, 441
- Cochlear scalae, 145, 438
- Cochlear structures, deformation, 49-51, 475
 elasticity, 467-480, 483, 510
 illumination, 34
 staining, 35
 visibility, 38, 426, 441, 459, 475
 volume displacement, 436
(See also Basilar membrane; Cochlear partition)
- Cochlear theory (*see* Auditory theory)
- Cochlear wall thickness, 443
- Cochlear windows, oval, 431
 pressure difference between, 105, 115-126
 round, 11, 431
 sealing, 21
- Cole, K. S., 654, 716
- Combination tones (*see* Difference tones)
- Comparison, of auditory and skin sensations, 249, 258-259, 275, 590-609, 622-623
 of direct and alternating potentials, 640
- Compression in semicircular canals, 147
(See also Bone conduction)
- Compressional waves, 128
- Concentration changes in cells, 232-236, 246, 255
- Conductive lesion, 88
- Conscious present, 369-378
- Consciousness lapse, 246, 371
- Consonance in skin sensations, 577
- Contrast, 208, 230, 255, 366, 417-419, 538, 610, 628-629
(See also Funnelling in nervous system)
- Coradi, G., 717
- Corti, A., 12, 717
- Corti's membrane (*see* Tectorial membrane)
- Corti's rods, 13
- Cotton, J. C., 80, 717
- Cotton plug as prosthesis, 108
- Cotton-plug attenuator, 63
- Cotugno, D., 470

- Coupling, for basilar membrane, 540-544
for series of resonators, 516, 519-521,
528-531
- Covell, W. P., 685, 717, 720
- Cow, cochlea, 507-508
eardrum, 194
- Crandall, I. B., 138, 269, 717
- Cremer, L., 387, 723
- Cross hearing, 86-87, 163, 174-176, 415
- Crowe, S. J., 717
- Curtis, H. J., 654, 716
- Dahmann, H., 717
- Damping, acoustic, in rooms, 381-383
in cochlea, 229, 232, 254-255, 404,
410-416, 458-460
by padded frame, 389
of resonators, 531
(*See also* Decay time; Logarithmic
decrement)
- Davis, H., 440, 493, 495, 512, 626, 641,
654, 685, 717, 725, 726
- Deafness, 88
concealment, 90-91
nerve, 624-625
simulated, 90
testing, 81-91
- Death, cell changes in, 651, 654
effect of, on cochlear partition, 494
on potentials, 641, 677, 689, 696,
700-701
- Decalcification, 22
- Decay intensity, 322-323, 329
- Decay time, 59-60
apparatus for determining, 58-60
for cochlea, 459-460
neural, 458
for sounds, 321-326, 329, 385-388,
393, 458, 535-536
for vibrations of membranes, 457
for vibratory sensations on skin, 458,
535-536
(*See also* Damping)
- Degrees of freedom of manipulators, 42
- Denker, A., 717
- Dental burr for dissection, 22
- Derbyshire, A. J., 685, 717
- De Trey's copper precipitate, 447
- De Vries, H., 486, 685, 695, 716, 717,
720
- Diestel, H. G., 551, 717
- Dietsch, G., 717
- Difference limen, auditory, 207-271
for amplitude, 207-208, 216-217,
220, 223, 228, 231, 248
under abnormal conditions, 624-
625
- Difference limen, for amplitude, method
of determining, 208, 211-212,
219-221
for frequency, 88, 220-223, 228, 231
for movement of sound source, 377
relations between amplitude and
frequency, 222-223, 227
for vibrations on skin, 249, 547, 562-
563
- Difference tones, 337-344, 361
effects of tensor tympani on, 343
- Differentiation of microphone current,
307-309
- Dijkgraaf, S., 485, 717
- Diplacusis, 601
- Dipole, voltage distribution about, 661-
666
- D-c fall, 639-640
- Direct potentials of cochlea, 636-647,
651-652
with perforating electrode, 688
- Direct and reflected sound fields, 332
- Direction, of motion of cochlear struc-
tures, 497
of sounds, 238, 250-254, 259, 272-301,
304-306, 318
of vibration in cochlear stimulation,
707-710
- Dispersion in fluids, 524-525
- Displacement, alternating, method of
producing, 49-51
- Dissecting instruments, 20-23
exchange, 44
- Dissection, capillary forces in, 26
methods, 19-22, 25, 28, 30, 40-42
(*See also* Manipulators)
- Distance between ears, 287
- Distance perception, for sounds, 280,
291, 301-313
effect of flow velocity on, 307-311
for vibratory sensations, 627
- Distortion, in ear, 218-219, 314-368, 577
of tones, 60-66
of waves by absorbent surfaces, 395-
398
- Distortion factor, 335
- Distraction effects, 246, 371
- Distribution, of judgments, 240-245
of potentials in cochlear fluids, 694-
695
- Doty, H. A., 717
- Drill, dental, for dissection, 23, 26, 32
use, 22, 430-431
- Drum membrane (*see* Eardrum)
- Drying, effects on middle ear, 96, 100
- Duckbill, cochlea, 486, 499
- Duplexity theory of hearing, 485

- Duration, of stimulation, effect of, on
sounds, 221-222, 236-238, 358,
554
on vibratory sensation, 559, 598,
620
of tones in music, 386-387
DuVerney, J. G., 444, 470, 717
- Ear, evolution, 249, 485-487, 500-510
Ear pads, use, 87
Eardrum, absence, 105-107, 116-117,
121-122, 304
artificial, 108, 193
effect of static forces on, 142, 304
elasticity, 96, 136-138, 142, 192-195
equal-amplitude curves for, 101
fibers, 95-96
impedance, 69-81, 110-112, 137-138,
141, 270, 312, 335-336
natural frequency, 101, 314-315
nonlinearity, 110, 335, 361
perforation, 108
postmortem changes, 482
structure and properties, 22, 96, 102,
195-198, 482
as velocity receiver, 312
vibratory action, 95, 100-101, 110-
112, 172-173, 192-193, 265, 314-
315, 319, 340, 360
Earphones, bone conduction from, 225
cushions for, 174
types, 174
Earplugs, 164, 176, 178-181
Earway attenuation, 164
Echoes, auditory, 557-558, 632
vibrational, on skin, 632-633
Eddies, in cochlea, 236, 256-257, 316,
366, 423-424, 428, 438-440
in relation to distortion, 337, 577
in cochlear models, 420-423
prevention, 445
Egan, J. P., 579, 717
Elasticity, of cochlear structures, 467-
480, 483, 510
of eardrum, 96, 136-138, 142, 192-195
Electrical analog of mechanical filter,
61-62
Electrical energy in cochlea, source, 635-
637, 642-647, 654
Electrical impedance of cochlea, 654-672
Electrical insulation in cochlea, 661,
686-687, 689, 694
Electrical resistance, of cochlea, 654-672
of fluid column, 671
Electrical stimulation of skin, 594-599,
608-609
- Electroanatomy of cochlea, 653-672,
685-686
Electrocapillary potentials, 677, 705-706
Electrodes, for d-c measurements, 644-
645
perforating, 688-692
vibrating, 672-684, 697, 702-705
Electronic switch, 58-60, 369-370
Elephant, cochlea, 508
sound analysis by, 508-509
Emde, F., 725
Emmermann, C., 717
End organs, interconnections, 550, 590-
591
Endolymph, 13
electrical conductivity, 692-694
Endolymphatic sac, 452
Energy balance of cochlea, 636-647
Energy density of sound in room for
reverberant field, 381
Energy flow, in cochlea, 512, 526
in wave motion, 510-524, 530-532
Energy source for bioelectric potentials of
ear, 635-639, 642-644
Engstrom, H., 717
Equal-loudness curves, 88-89, 208-209,
216-218, 264
Equal-magnitude curve for skin, 566
Equilibrium, effect of tones on, 424
Errors, experimental, 7-9
observational, 239
Esser, M. H. M., 192, 717
Eustachian tube, 11
click produced by, 314-315
Ewald, J. R., 354, 404, 405, 410, 428,
438, 541, 550, 717
Ewald's model of cochlea, 407, 438
Ewald's theory (*see* Standing-wave
theory)
Excitation, 207, 217, 228-236, 239-240,
246, 255
sharpening up, 223, 538-539, 556-557
Exner, S., 717
Experimental errors, 7-9
Exploring-tone method, 87, 332-333,
336
External auditory meatus, 11, 20
congenital closure, 304
effect of closing, 134-142, 146, 160-
161
effect on sound field, 267-271
effect of static pressure in, 141-142,
146
method of opening, 30
open versus closed, 135-142, 144-146,
160-161
resonance, 84, 270-271
Eyring, C. F., 369, 718

- Facial canal, 430-431
 Fader circuit, 58-60, 369-370
 Fahrenheit, S., 151, 718
 Familiarity, effect on sound localization, 292
 Fatigue, auditory, 88-90, 275, 354-368
 for beating tones, 352, 536
 bilateral effects, 363
 effect of, on loudness, 208-209, 225-226, 276, 355-358
 on overtones, 337-338
 on pitch, 367-368
 on sensitivity, 207-211, 536
 on transient processes, 328
 effect on, of eardrum tension, 362
 of stimulus duration, 353-357
 frequency selectivity, 256, 353-356, 365-367
 loudness-doubling method, 362-363
 place of origin, 354, 359, 362, 364
 recovery from, 357-358
 relation, to sound direction, 276
 to sound intensity, 356-357, 364
 temporal course, 357, 363-365
 tactual, 259, 354, 627
 Fechner, G. T., 238, 718
 Fechner's laws, 238, 246, 250-257, 370
 Feeling sensations, localization, 219
 Feeling threshold, 113, 219-220, 257, 464
 Fenestration, 122-124, 164
 Fernández, C., 717
 Filters, mechanical, 60-66, 161-162
 Firestone, F. A., 104, 150, 165, 349, 716, 718
 Fischer, F. A., 181, 719
 Fischer, J., 715
 Fischer, M. H., 718
 Fischer, O., 419, 718
 Fish, lateral line, 485
 macular stimulation in, 703
 Fitzhugh, R., 612, 715
 Fixation of tissues, 12-13, 17-18
 Flanders, P. B., 718
 Fletcher, H., 219, 261, 263, 301, 483, 584, 718
 Flottorp, G., 588, 723
 Flow velocity, effect on distance perception, 307-311
 Fluid columns of cochlea, 427, 444, 458
 Fluid displacement in cochlea, minimizing, 202
 Fluid loading, 446
 Fluid pathways of cochlea, 104, 106
 Fluid potentiometer, 347-348
 Fluid pulsator for cochlear stimulation, 695-696
 Fluid streaming, in cochlea (*see* Eddies)
 in the semicircular canals, 423-424
 Foramen jugularis, 430
 Form, of sound-pressure stimulation,
 effect on timbre, 319-320
 of vibratory sensations, 591, 598-599, 613, 619
 effects of fatigue on, 627
 Fourier integral, 75
 Fourier's principle, 72, 622
 Fowler, E. P., 718
 Fowler's recruitment test, 88
 Frahm frequency meter, 413, 494-495
 Frank, O., 96, 111, 192, 315, 718
 French, N. R., 718
 Frequency analysis in cochlea, 60, 404, 410-416, 428-429, 500-510, 535-539
 Frey, M. von, 259, 354, 718
 Frey, von, hairs, 23, 467-472
 Fricke, W., 717
 Frocht, M., 199, 718
 Frog, ear, 181, 199
 vocalization, 181
 Frog skin, nerve volleys from, 587
 Fumagalli, Z., 718
 Funneling in nervous system, 609-613, 627-634
 Fusion, critical frequency, for ear, 413-414
 for skin vibrations, 599-601
 Galambos, R., 612, 718
 Gardner, M. B., 725
 Garten, S., 718
 Gatty, O., 654, 718
 Gaussian law, 239
 Geffcken, W., 66, 69, 112, 203, 258, 312, 336, 718
 Geiger, P. H., 349, 718
 Geldard, F. A., 564, 719
 Gerard, R. W., 649
 Gerdien, H., 162, 719
 Gerlach, E., 52, 719
 Gernandt, B. E., 685, 717
 Giesswein, M., 140, 725
 Gildemeister, M., 719
 Glass windows for observing structures, 32
 Goldberg, E., 719
 Goldman, A., 354, 718
 Grass, absorption of sound by, 396-398
 Gray, A. A., 719, 728
 Gray, T. S., 75, 719
 Grimm, K., 719
 Groot, P. D., 725
 Grounding pathway of cochlea, 660-661
 Group velocity of cochlear waves, 403
 Grouping of sounds, 373

- Growth of sensations (*see* Duration of stimulation)
- Guild, S. R., 685, 717, 719, 720
- Guinea pig, cochlea, 443, 502-504
eardrum, 196
organ of Corti, 487
sound analysis by, 503-504
- Gullstrand, A., 35
- Haas, H., 632, 719
- Hähnle, W., 150, 719
- Hahnemann, W., 267, 719
- Hair cells, 13
anoxic changes in, 708
excitation, 128
inner, 486
movement, 498-500
number, 619
rows, 486
- Hair probes, 23, 467-472
- Hallpike, C. S., 654, 685, 719
- Hamilton's principle, 512, 533
- Hammer, 11
function of head, 102, 181, 201
- Hardesty, I., 468, 719
- Harmonic analyzer, 75-78
- Harmonics, 578
in ear, 99, 332-338
in skin vibrations, 577-590
- Harris, J. D., 622, 719
- Hartline, H. K., 612, 719
- Hartmann-Kempf, R., 548, 719
- Hartridge, H., 411-412, 719
- Hasse, C., 485, 486, 719
- Hausmann, T., 719
- Head, action of sound on, 163
determination of center, 286
effect of sound field on, 267-271
- Head movements, effects, 72
during walking, 191
- Headrest, 72
- Hearing, tests, 81-91, 135, 148
theories, 443-446, 539-546
- Hecht, H., 181, 267, 719
- Heisig, H., 134, 138, 267, 727
- Held, H., 404, 464-466, 719
- Helicotrema, 12, 257, 316, 469, 475
- Helmholtz, H. L. F., 11, 95, 115, 117, 261, 348, 350, 352, 404, 413, 444, 468, 471, 535, 574-576, 677, 719
- Helmholtz resonance theory (*see* Resonance theories)
- Hemphill, R. W., 641, 728
- Hensen, V., 468, 470, 720
- Hensen cells, 16, 490-491
- Herzog, H., 145, 720
- Hilding, A. C., 720
- Histological techniques, 12-13, 17-18, 22, 35, 488
- Holst, E. von, 703, 720
- Hood, J. D., 719
- Hooke's law, 680
- Hornbostel, E. M. von., 107, 225, 253, 254, 285, 287, 295, 301, 317, 349, 720
- Hornbostel formula, 279
- Hornbostel-Wertheimer constant, 253-254, 274
effect of fatigue on, 278, 280
- Hort, W., 720
- Howe, H. A., 685, 720
- "Hütte," 473, 648, 720
- Huggins, W. H., 720
- Hughes apparatus, 355
- Huizing, H. C., 720
- Hunt, R. S., 720
- Hurst, C. H., 405, 720
- Hydrodynamic theories of cochlea, 444
- Hypertension of cochlea, 587
- Illumination, 34
stroboscopic, 37-40, 422, 427, 441
- Impedance, acoustic, for capillary, 138
for cavity, 137
for ear, 72, 137, 269-270
method of measuring, 68-81
for mouth opening, 73
phase of, 70-72
electrical, of cochlea, 654-672
(*See also* Capacity of cochlear membranes)
mechanical, matching in inner ear, 492-493
method of measuring, 33-34, 49-51, 478
- Impedance matching in organ of Corti, 492-493
- Impulse method (*see* Pulse method)
- Incisors, clicking, 168
- Incudostapedial joint, 201-202
- Incus, 11
(*See also* Ossicles)
- Infections, 20-21
- Inhibition, 609-613
in nervous system, 547, 557-560, 571
for skin sensitivity, 569-570, 596-609
(*See also* Contrast; Funneling in nervous system)
- Injury to tissues in dissection, 26
- Inner ear, maximum bearable static pressure in, 433-434
- Inner hair cells, 486
- Innervation density, 564-566
- Insects, auditory organ, 619

- Instruments, dissecting, 20-23, 44
 Insulation in cochlea, 666-672
 Integrator, 75
 Integration of microphone current, 307-309
 Intelligibility of syllables, 379-380
 Intensities, auditory and tactual compared, 249
 Interactions, between binaural tones, 605-606
 of sounds, suppression of reverberation, 374-376
 between two vibratory frequencies, 606-607
 Interference tube, 333, 335
 Internal resistance of middle ear, 104
 Interval between stimuli, effects, 213, 215, 328
 Intervening image, 319
 Itching, 262
- Jäderholm, G. A., 717
 Janovsky, W., 335, 339, 348, 525, 720
 Janus green B as vital stain, 488
 Jälof, R., 720
 Johnson, K. S., 720
 Jones, I. H., 134, 138, 148, 158, 720, 721
 Judgment theory, 213-214
 Judgments, distribution, 240-245
 Jugular foramen, 430
 Junction potential, 649
 Jung, H., 458, 556, 720
- Kahler, O., 717
 Kato, T., 216, 720
 Katsuki, Y., 720
 Katz, D., 564, 571, 720
 Keibs, L., 66, 148, 433, 718, 727
 Keidel, L., 723
 Keidel, W. D., 587, 591, 601, 720-721
 Keith, A., 114
 Kerekes, G., 721
 Kessel, J., 359, 360, 721, 722
 Kingsbury, B. A., 88, 209, 263, 365, 721
 Kircher, A., 10, 721
 Kleinknecht, F., 464-465, 501, 719, 721
 Klemm, O., 568, 721
 Kluge, J., 151, 718
 Klumpp, R. G., 579, 717
 Knudsen, V. O., 134, 138, 148, 158, 164, 178, 179, 208, 211, 222, 231, 247-249, 369, 383, 387, 564, 720, 721, 727
 Kobrak, H. G., 721
 Köhler, W., 108, 213, 241, 361, 721
 Köhler's theory of comparison, 213
 Kölliker, A., 721
- Kohler, I., 574, 721
 Kolmer, W., 14, 721
 Kopac, M. J., 716
 Krause, W., 17, 721
 Kreuzer, B., 369, 723
 Kucharski, P., 721
 Kühl, A., 417, 721
 Kufler, S. W., 612, 715, 721
 Kuhl, W., 95, 721
 Kuile, E. ter, 355, 366, 368, 405, 487, 493, 703, 721
 Kupfer, E., 677, 721
 Kurtz, R., 148, 722
- Labyrinth, 275, 500-501
 Landes, G., 722
 Landmarks, anatomical, 19-20, 30
 Lane, C. E., 87, 139, 163, 265, 332, 414-415, 417, 722, 727
 Lane's method of best beats, 87, 176, 333, 336
 Lange, B., 722
 Langenbeck, B., 108, 138, 267, 269, 722
 Latencies for skin stimulation, 601-602
 Lateral-line organ, 485
 Lateralization of skin sensations, 572-573, 630-632
 (See also Location of vibratory sensations)
 Law of contrast, 208, 230, 255, 366, 417-419, 538, 610, 628-629
 (See also Funnelling in nervous system)
 Lawrence, M., 512, 526, 533, 577, 641, 722, 727, 728
 Legoux, J. P., 493, 495, 512, 577, 716, 722, 726
 Lehmann, A., 246, 247, 722
 Lehner, S., 447, 722
 Lever principle of impedance matching, 493
 Lewicki, G., 415, 715
 Lewis, D., 722
 Lichte, H., 169, 722
 Licklider, J. C. R., 512, 720, 722
 Lifschitz, S., 332, 389, 722
 Ligaments of middle ear, function, 113
 Limits, methodological, 9-10
 Lincke, C. G., 12, 722
 Linckh, H. E., 151, 718
 Lindsay, R. B., 60, 137, 726
 Linearity, in cochlea, 481
 in middle ear, 266
 (See also Distortion)
 Ling, G., 648, 722
 Lip, sensitivity to vibration on, 445
 Lippmann, G., 722
 Litharge-glycerin cement, 447

- Lizard, basilar membrane, 486
 Loading, 51
 for basilar membrane, 445-446, 496
 Localization of response in cochlea,
 440-442, 463
 (See also Basilar membrane, patterns of
 response along)
 Location, of sound image, 289-290, 292,
 294-297
 of sounds, 292, 299-302, 374, 573, 632
 of vibratory sensations, 560-562, 573,
 597, 630-632
 Logarithmic decrement, 411
 for ear, 254, 354, 404, 458-459
 for skin vibrations, 166
 (See also Damping)
 Lohmann, W., 722
 Loop resistance of cochlear scalae,
 671-672
 Loudness, absolute, 215
 at absolute threshold, 245
 for binaural stimulation, 223-226, 417
 decay, 322-323, 458
 effect on, of duration, 236-238, 358
 of fatigue, 208-209, 225-226, 276,
 355-358
 of static pressure (see Static pres-
 sure, in meatus)
 effect on pitch, 463-464
 theory, 227, 239, 245, 247
 at tickle threshold, 263
 Loudness variations in alternating tones,
 537-538
 Loudspeaker directionality, 388-389
 Low tones, 60-69
 Lower jaw in bone conduction, 129,
 143-144
 Lower limit of pitch, 258, 260-261
 Lowy, K., 484, 722
 Lumping of properties, 19
 Lurie, M. H., 685, 717, 726
 Lux, F., 427, 443, 722
 Lux theory of fluid columns, 427, 444, 458

 MacAuliffe, D. R., 717
 McClung, C. E., 42, 722
 Maceration, 22
 Mach, E., 140, 417, 538, 722
 Mach's law of contrast (see Contrast)
 MacNair, W. A., 387, 722
 Macula utriculi, 452
 stimulation, 678
 Mader, O., 722
 Mader's analyzer, 76-78
 Magnitude of sensation, 245
 for vibrations on skin, 615-626
 Malingering, 90-91

 Malleus, 11
 function of head, 102, 181, 201
 Mandible in bone conduction, 129,
 143-144
 Mangold, E., 359, 722
 Manipulators, 40-49, 674-675
 Manometer, membrane, 61, 257
 Maré, G. de, 485, 723
 Mark, H., 277, 715
 Marks, L. S., 723
 Markus, J., 667, 723
 Martin, H., 723
 Martin's equation, 337
 Masking, 265-266, 317, 321, 333-334,
 414-415
 in audiometry, 82, 86-88, 139, 163
 Mastoid operation, effects on bone con-
 duction, 162-163
 Mastoid process, 133, 430-431
 Maxfield, T., 302, 723
 Mayer, O., 723
 Meatus, auditory (see External auditory
 meatus)
 Mechanical filter, electrical analog, 61-62
 Mechanical shock, effect on cochlear
 partition, 642
 Membrane of Corti (see Tectorial
 membrane)
 Membranes, action of clicks on, 457
 effects on, of bioelectrical fields,
 635-636
 of pressure, 472
 measurement of volume displacements
 in, 478-479
 Mercury-arc lamp, 37
 Method of constant stimuli, 211-212, 240
 Methodological limits, 9-10
 Methodology, 3-10, 33-91
 Methylene blue, 488
 Metz, O., 723
 Meyer, E., 138, 300, 302, 332, 369, 387,
 723
 Meyer, Max F., 355, 366, 368, 405
 Meyers, C. K., 622, 719
 Micksch, K., 447, 723
 Micromanipulators, 40-49, 674-675
 Microphone for vibration measurement,
 151-155, 164-177
 Microphonics, cochlear (see Cochlear
 microphonics)
 Micropipettes, 647-653
 positioning, 35
 Microscope, adjustment, 25, 36
 stereoscopic, 35-36
 Middle ear, compression, 202
 effects of disease on, 99-101
 model, 124-126

- Middle-ear apparatus, absence, 122
 action, 95-126
 natural frequency, 111
 nonlinearity, 110, 114, 197, 343
 protection, 112-113
 resistance, 103-104
 (See also Static pressure, in meatus)
 Middle-ear cavity, method of exposing,
 30
 resonance in, 117
 volume, 109-110, 200
 Middle-ear ligaments, 113
 Middle-ear muscles, bilateral action, 216
 effect on eardrum tension, 336
 friction in, 104
 function, 113-114, 203
 Mirror cemented to eardrum or manu-
 brium, 108-109
 Models, cochlear (see Cochlear models)
 middle-ear, 124-126
 for resonance theory, 545-546
 for traveling-wave theory, 545-547,
 550-568
 Modiolus 12, 475
 Modulation, 222-223, 266-267, 336, 345
 effect of, on difference tones, 344
 on sound direction, 299-300
 in vacuum tube, 336
 Moe, C. R., 584, 723
 Mosaic method, 4
 Mouse, cochlea, 506
 sound analysis by, 506
 Mouth, sound pressure near, 183-186
 Mouth cavity, resonance in, 172
 Movements, observation, 37-40
 of persons in room, effect on reverbera-
 tion, 392
 Müller, J., 114, 162, 723
 Munson, W. A., 263, 718
 Music, duration of tones in, 386-387
 effects of reverberation on, 369,
 389-392
 intensity of playing, 380
 Musical instruments, changes of timbre
 in, 332

 Natural frequencies of vibratory systems,
 477-478
 Natural rhythm, 371-373
 Nature of auditory stimulus, 703
 Negative experiments, 7
 Nernst, W., 233, 649, 723
 Nernst's law of nerve excitation, 236,
 247
 Nerve deafness, 88-89, 624-625
 Nerve discharge in sound localization,
 287-288

 Nerve endings, 207, 229
 Nerve excitation, 207, 217, 228-236,
 239-240, 246, 255
 Nerve fibers, auditory, 15
 interaction among, 218
 Nerve impulses, maximum frequency, 265
 synchrony for skin, 593, 595-596,
 601-602
 Nerve potentials, effect of anoxia on, 641
 Neubert, K., 487, 723
 Neural decay time, 458
 Neural pathways for skin, 570
 Neural plexus, 550, 590-591
 Neural volleys, 590-603
 Newman, E. B., 577, 726
 Noether, F., 60, 727
 Noise, effect on thresholds, 191
 Nonlinearity of ear (see Distortion;
 Harmonics)
 Nonpolarizable electrodes, 655
 Numerical values for cochlea, 403

 Observational errors, 239
 Observers, 6, 243-246, 613-614
 Ohm, G. S., 471, 723
 Ohm's law, 471
 Olson, F., 369, 723
 Olson, H. F., 723
 Onset of sound, 383-384
 Onset intensity, 322, 326, 329-330
 Onset processes, 326-328
 Onset time, 322, 326-327, 536
 apparatus for determining, 58-60
 difference limen for, 326-331
 Onset transients, 320-321, 331, 383
 (See also Onset processes)
 Opening cochlea, effect of, 483
 Opheim, O., 588, 723
 Organ of Corti, 12, 15-16
 elasticity, 468, 487-492
 fine structure, 485-493
 impedance matching by, 492-493
 number of hair cells in, 619
 shearing forces in, 493
 wave motion in, 496-500
 Orientation, anatomical, 30-32
 of pipette, 35
 Osmotic pressure in sense cells, 233
 Ossicles, auditory, 95-102, 197-201
 forms of motion, 112-113, 197-201,
 265
 functions, 181, 196-197, 200-201
 lever action, 95-100
 mobility, 433
 resonance, 163
 (See also Incus; Malleus; Stapes)
 Otosclerosis operation, 122-124, 164

- Oval window, 431
 - (See also Cochlear windows)
- Overstimulation, 112, 257, 481, 498, 640
- Overtone, 578
 - in ear, 99, 332-338
 - in skin vibrations, 577-590
- Oxygen concentration effects, 488
- Oxygen deprivation, 640-642, 645, 654, 677, 682, 689, 700
- Pain, effect on sensitivity, 246
- Pain threshold, 14, 481
- Paradoxical waves, 510-524, 532-533
- Particle velocity, 306-307
 - perception, 305-312
- Pascal, B., 511
- Pathological conditions in cochlea, 533-534
- Pattie, F. A., Jr., 278, 724
- Pauli, H., 719
- Pauli, R., 211, 724
- Pendulum model of cochlea, 519, 526-534, 542-543
- Penfield, W., 565, 724
- Perception reversals, 281, 371
- Perceptive lesion, 88-89
- Percussion method, 74
 - (See also Pulse method)
- Perforating electrode, 688-692
- Perforations of membranes, 647-648, 652-653, 686
 - effects on cochlear potentials, 697-699
 - in models, 409-410
- Perilymph, electrical conductivity, 671, 693-694
 - viscosity, 406-407, 439
- Perilymph pressure, effect of anesthesia on, 688
- Perilymphatic duct, 452
- Periodicity, of nerve discharge, in beats, 587
 - in sound localization, 287-288
 - in reversals of perception, 371
- Persistence (see Decay time)
- Perspective, reversible, 281, 371
- Persson, C. R., 716
- Peterson, L. C., 526, 666, 724
- Phase changes produced by ear, 70-72
- Phase measurement, 38-40
- Phase-measuring stroboscope, 461
- Phase relations, in basilar membrane movements, 460-463, 494
 - in cochlear potentials, 689-690
 - in ears without eardrum, 107
 - in movements of middle ear and cochlea, 432-433
 - for round-window membrane, 436
- Phase shift, effect on cochlear resonators, 411-413
- Phase shifter, 412, 602-603
- Phonation (see Vocalization)
- Photoelectric siren, 461
- Pickup, 151-155, 164-177
- Pillar cells, 13
- Pinna reflex, 501
- Pistonphone, 258
- Pitch, analogy in skin sensations, 562
 - basis, 590
 - effect on, of duration, 221-222
 - of loudness, 463-464
 - lower limit, 258, 260-261
- Pitch-loudness interval, 246
- Place of origin of cochlear microphonics, 635-636, 684-710
- Planck, M., 649, 724
- Plastic-tube model of cochlea, 546-547, 550-568, 575-576, 584-587
- Platinum black, 655
- Pneumatization, 124-126
- Pohl, R. W., 724
- Poiseuille's law, 138, 406-407, 435
- Polarity of microphonics within cochlea, 707-709
- Polarization in cochlea, 656-657
- Politzer, A., 13, 14, 724
- Pollack, I., 622, 724
- Polvogt, L. M., 717
- Postmortem changes in tissues, 482-483
- Pouillet, C. S. M., 114, 162, 723
- Pressure, alternating, production, 49-51
 - sense of, 249
 - static, action, on inner ear, 433-434, 472-476
 - on middle ear, 99-100, 142, 336, 342-343, 359-361
- Pressure cell, 151-156, 164-177
- Pressure difference, between cochlear windows, 117-126, 434-435
 - from fluid streaming, 11
 - in nerve excitation, 233
- Pressure effect of needle on membrane, 679
- Pressure receiver, ear as, 331
- Pressure transformation in ear, 95-103, 115-116
- Preyer's reflex, 501
- Pricking in ear, 219, 262-263
- Prickle, 594
- Principle of maximum stimulation, 419
- Pritchard, U., 486, 724
- Probe, capacitative, 53-57
 - vibrating, 51
- Problems, nature and origin, 4-5
- Procopiu, S., 677, 724

- Protection of ear, 102, 113-114, 203, 219, 265
- Pulse, circulatory, effect on skin sensations, 613
- Pulse method, 72-81, 164, 168
- Pulses, acoustic, loudness variations, 537-538
 - in reverberant room, 384, 386
 - production, 78-79
 - velocity in cochlea, 456-457
 - (*See also* Clicks)
- Quanta of sensation, 238-245, 254, 260-261
- Quantification, 6
- Quartz crystal, 152-155
- Quinke, G., 677, 724
- Quinke interference tube, 333-335
- "R" character, 345, 346
- "R" sound, 336
- Rabinovich, A. V., 302, 724
- Radial fibers of eardrum, 95-96
- Radiator of zero order, 305
- Radius of action on skin, 616-617, 631
- Random noise, effect on skin sensations, 619-620, 629-630
- Randomizing switch, 212
- Ranke, O. F., 439, 485, 724
- Ranvier, L., 14, 724
- Rasmussen, T., 724
- Rat, cochlea, 506-507
 - sound analysis by, 506-507
- Rawdon-Smith, A. F., 654, 685, 719
- Rayleigh, Lord, 117, 269, 724
- Rayleigh waves, 495
- Receivers, bone-conduction, 133-134, 150-151, 158-159
- Reciprocity method, 117-126
- Reciprocity principle, 117
- Recruitment, 88, 210
- Rectification in cochlea, 361
 - (*See also* Distortion)
- Reference tone, 231
- Reflecting surfaces, breaking up, 376
- Reissner's membrane, 13, 407
 - coupling to basilar membrane, 497
 - elasticity, 467
 - as source of cochlear potentials, 695
- Rejtö, A., 145, 724
- Renaut, J., 14, 724
- Resistance measurement, 655-660
- Resolving power (*see* Selectivity of basilar membrane response)
- Resonance, of cochlear partition, 454-455, 460-462, 494, 504-510
 - Resonance, discovery, 470
 - in rooms, 383-384
 - sharpness (*see* Selectivity of basilar membrane response)
 - Resonance theories, 254-255, 354, 366, 404, 481, 526, 540-545, 549
 - forms, 444
 - history, 444
 - model for, 545-546
 - Resonant circuit, 369-370
 - Resonators, cavity, construction, 80-81
 - Resting potentials of cochlea, 636-647, 651-652
 - with perforating electrode, 688
 - Reticular membrane, 14, 16, 490-492
 - Rettinger, M., 724
 - Retzius, G., 14, 486, 724
 - Reverberation, 369-383
 - effect of, on apparent distance of sound, 302-303
 - on music, 369, 389-392
 - effect on, of persons moving in room, 392
 - relation to rhythm, 373
 - suppression, 374-376
 - Reverberation onset process, 331
 - Reverberation time, 321, 369-383, 389-392
 - Reverberation transients of room, 331
 - Reversals of perception, 281, 371
 - Reversible perspective, 281, 371
 - Reynolds, O., 724
 - Rhythm, 371-373
 - Riegger, H., 555, 724
 - Riegger's half-resonance curve method, 155-156
 - Riesco-MacClure, J. S., 685, 717
 - Riesenfeld, E. H., 233, 723
 - Riesz, R. R., 208, 211, 231, 234, 261, 348, 724
 - Rinne test, 148
 - Roaf, H. E., 443, 724
 - Roberts, W. H., 564, 724
 - Robinson, C., 724
 - Rods of Corti, 13
 - Rohracher, H., 725
 - Room, natural frequency, 383-384
 - Room acoustics, 302, 321-322, 331-332, 369-399
 - Rooster, anatomy of ear, 196-198
 - sensitivity to own vocalizations, 183-184
 - Ross, D. A., 728
 - Rotary spark gap, 456
 - Rotating phase shifter, 602-603
 - Rotating skin sensations, 574, 600-605, 631-632
 - Rotating tones, 300, 349, 605, 631

- Roughness, acoustic, 344-353
 Round window, 11, 431
 Round-window membrane, 429-438
 phase relations for, 436
 volume elasticity, 435-438
 Roux, W., 472, 725
 Ruch, T. C., 590, 591, 725
 Runge, C., 725
 Rutherford, W., 550, 725
- Sabine, W. C., 60, 321, 322, 381, 389, 394, 725
 Sabine reverberation time, 374, 382
 Sacculæ, 452
 stimulation, 678
 Sacia, C. F., 725
 Safranin O as vital stain, 489
 Saul, L. J., 641, 685, 717, 725
 Scala tympani, 11
 Scala vestibuli, 11
 Schäfer, H. L., 140, 725
 Schellhammer, G. C., 10, 725
 Schmidt, H. G., 721
 Schmiescheck, U., 475, 725
 Schouten, J. F., 39, 725
 Schütz, E., 726
 Schuster, K., 73, 321, 332, 369, 725, 727
 Schwabach test, 148
 Schwarz, 129, 725
 Screwdriver used as manipulator, 40-42
 Second-order microphonics, 696, 701
 Selectivity of basilar membrane response, 404, 410-416, 446-449, 454-455, 504-510, 535-537
 (See also Cochlea, as frequency analyzer)
 Sell, H., 155, 725
 Semicircular canal, 11
 opening, 22
 Sensitivity, effect of pain on, 246
 (See also Thresholds)
 of skin (see Skin sensitivity; Vibratory sensitivity of skin)
 Sensory cells (see Hair cells)
 Sensory quanta, 238-245, 254, 260-261
 Shambaugh, G. E., 725
 Sharpening up of excitation, 223, 228-231, 538-539, 556-557
 Shearing forces in organ of Corti, 493
 as sensory stimuli, 703-708
 Sheep, eardrum, 194
 Sherrington, C., 611, 725
 Shickman, G. M., 619, 726
 Shielding, electrical, 160
 Shock effect on cochlear partition, 642
 Shock waves in cochlea, 456-457
 Silver crystals, use, 38, 441, 459, 475
- Simulated deafness, 90
 Sivian, L. J., 69, 725
 Size, apparent, of auditory sensations, 377, 607
 of skin sensations, 607
 Skin, in bone conduction, 130, 133-134
 compared with ear, 564-634
 mechanical properties, 148-150, 156-158, 164, 166
 stimulation, areal, 617-618, 622-625
 by clicks, 621-622, 629-631
 latencies in, 601-602
 two-point, 566, 615-616
 Skin sensations, effects of rate of loading on, 558
 (See also Vibratory sensitivity)
 Skin sensitivity, effect on, of adhesive tape, 617-618
 of warming, 626-627
 (See also Vibratory sensitivity of skin)
 Skramlik, E. von, 564, 725
 Skudrzyk, E., 725
 Skull, location in, of ear, 199-201
 of middle ear, 199-201
 motion during walking, 191
 rotation in vocalization 190
 vibrations in response to sounds, 129-131, 163-181, 189
- Slit lamp, 34
 Snake, basilar membrane, 486
 Snow, W., 302, 725
 Soest, J. L., 725
 Sound, spatial attributes, 272-313
 Sound fields, direct and reflected, 332
 effect of absorbent surface on, 392-399
 measurement, 378-381
 relation to room size, 382
 Sound image of Ewald (see Standing-wave theory)
 Sound images, aftereffects in, 277
 for bone-conducted tones, 143
 changes in time, 277
 displacement threshold, 250-254
 fusion, 289-290, 292, 294-297
 interaction, 288-289
 latencies, 292
 location, 289-290, 292, 294-297
 paths followed by, 278-286
 size, 377
 Sound-level meter, 378-379
 Sound location, 292, 299-302, 374
 nerve discharge in, 287-288
 (See also Sound images, location)
 Sound-outflow theory, 140
 Sound pathways, 278-286
 Sound-pattern theory, 354, 365, 404-405, 428, 438, 481, 540-545
 Sound pulses (see Pulses)

- Sound transmission, 192, 196-197
(*See also* Middle-ear apparatus;
Ossicles)
- Space, relation of tactual and auditory,
275
- Spandöck, F., 525, 720
- Spark apparatus, 79-80
- Spatial attitude in suppression of sound,
375
- Specificity (*see* Selectivity of basilar
membrane response)
- Speech, intelligibility, 369
regulation, 379
intensity, 379
- Sphere, as sound source, 305-306
vibrations, 169-172
- Spiral diagrams of cochlea, 503-508
- Spiral ligament, 16
- Spiral limbus, elasticity, 472
- Spiral vessel, 487
- Spoor, A., 720
- Spread of vibratory sensations on skin,
571-572
- Square waves, roughness, 351-352
- Staining of tissues, effects of oxygen
concentration on, 488
vital, 35, 488-489
- Standardization of instruments, 23, 44
- Standing-wave theory, 354, 365, 404-405,
428, 438, 481, 540-545
- Standing waves in cochlea, 354, 365,
404-405, 428, 438, 481, 540-545
- Stapes, 11
amplitudes of vibration as function of
frequency, 103, 172-174
artificial, 427, 482
fixation, 143, 145
footplate area, 102
force required for extraction, 434
mobility, 435
modes of motion, 112-113, 201-203,
482
position, 115
as source of difference tones, 344
spatial relation to basilar membrane,
256-257
transients, 316
- Static pressure, action on basilar mem-
brane, 472-476
maximum bearable, in inner ear,
433-434
in meatus, 99-100, 141-142, 336,
342-343, 359-361
- Steinberg, I., 302, 725
- Steinberg, J. C., 718, 725
- Step process, 74
- Stereophonic hearing, 566-568
analogy for skin, 566-568
- Stern, W. L., 371, 725
- Steudel, U., 320, 458, 726
- Stevens, S. S., 440, 463, 577, 619, 626,
654, 726
- Stewart, G. W., 60, 137, 726
- Stirrup (*see* Stapes)
- Straut, C. B., 641, 728
- Streaming of fluid in cochlea, 11
(*See also* Eddies)
- Streaming potentials, 677
- Stretched-membrane principle of imped-
ance matching, 492-493
- Stria vascularis, 16
- Stroboscope, 37-40, 461
- Stroboscopic illumination, 422, 427, 441
- Strutt, M. J. O., 113, 369, 383, 387, 394,
726
- Stuhlman, O., Jr., 99, 197, 726
- Stumpf, C., 225, 291, 332, 348, 575, 576,
726
- Styloid process, 430
- Subharmonics, 114, 197, 476
- Subjects, 6, 243-246, 613-614
- Substitution method of measuring
impedance, 69-70
- Summation, 609-613, 625-626
binaural, 219, 223-226, 235
of intensity for touch, 569-570
of loudness, 416-417
region for skin, 616-617, 631
of vibratory sensations on skin, 597, 626
(*See also* Funneling in nervous system)
- Suppression, in nervous system, 292-294
of sound, 375
- Swallowing, clicks produced by, 314
effect on middle-ear pressure, 342
- Switch, electronic, 58-60, 369-370
randomizing, 212
- Syllables, number in words, 371
- Sympathetic vibration (*see* Resonance)
- Synchrony of nerve discharges from skin,
593, 595-596, 601-602
- Tactual and auditory space relation, 275
- Tasaki, I., 493, 495, 512, 726
- Taylor, S., 576, 726
- Techniques, anatomical, 12-13, 17-32,
34, 49
- Tectorial membrane, 14-17, 468-469
elasticity, 467-469, 489-491
- Telephone theory, 481, 540-546
model for, 545-546
- Temporal bone dissection, 20-22, 30
- Tensor tympani muscle, 112, 114
contraction, 359, 361
effects of, on difference tones, 343
on ossicles, 343

- Tensor veli palatini muscle, 314
- Tests of hearing, clinical, 88, 135, 148, 163
- Theater, paths of sound in, 393-394, 558
- Theoretical method, 4
- Theories of hearing (*see* Duplexity theory of hearing; Resonance theories; Standing-wave theory; Telephone theory; Traveling-wave theory)
- Thermophone, 66-69, 317
- Thermostat, 43
- Thévenin, L., 726
- Thévenin's theorem, 104
- Thoma, A., 720
- Threshold, absolute, for skin, 566, 583
 absolute intensity, by air conduction, abnormal, 88-91, 106, 162
 for low tones, 257-261
 normal, 84-85, 106, 246, 248, 455
 with vibrator, 136
 by bone conduction, 131-136, 148, 160-162, 172-173, 191-192
 conditions affecting, 207, 246
 reproducibility, 83-85, 433
 (*See also* Audiogram)
 differential (*see* Difference limen)
 of feeling, 113, 219-220, 257, 464
 of fusion, 260-261
- Tickle, 262-264
 threshold, 114, 261, 264
- Timbre, basis, 320
 effect on distance perception, 313
 effect of intensity on, 218
 for interrupted tones, 387-388
 just-noticeable differences in, 335
- Time delay between two stimuli, effect of,
 for ear, 573, 632
 for vibration on skin, 573, 630-632
 (*See also* Location)
- Time differences perceived by skin, 568
- Timoshenko, S., 337, 726
- Tinnitus, 88-89
- Tischner, H., 726
- Todd, B., 726
- Tonal fusion (*see* Fusion)
- Tonal gap, 464-465
- Tortoise, basilar membrane, 485-486, 501
 labyrinth, 501
- Touch produced by low tones, 258-262
- Tower, O. F., 649, 726
- Transformer action in ear, 95-126
- Transient intensity, 322, 328-330
- Transient processes, 322
- Transient time, 322, 328
- Transients, apparatus for producing, 58-60
 audibility, 321-332
- Transients, in cochlear models, 555-556, 558
 of mouth cavity, 80
 in ossicular movements, 81
 patterns on basilar membrane produced by, 542, 549
 in room acoustics, 331-332
 (*See also* Decay time; Onset time)
- Transmission characteristics, 95
 in ear, 72-81, 95-126, 429-433, 437
 (*See also* Impedance)
- Transmission lines, mechanical analogies, 514
- Trautwein, F., 393, 726
- Traveling-wave theory, 540-541, 544-549
 model for, 545-547, 550-568
- Traveling waves, in cochlea, 425, 461, 494, 512
 in cochlear models, 517-524
 in series of resonators, 542-543
 in skull, 169
 in transmission line, 512-515
- Trendelenburg, F., 265, 555, 719, 726
- Trills, 254, 413-414
- Tröger, J., 69, 137, 270, 289, 312, 726
- Tschachotin, S., 726
- Tschermak-Seysenegg, A. von, 538, 726
- Tuned reeds (*see* Cochlear model)
- Tuning-fork tests (*see* Bone conduction; Clinical tests of hearing)
- Turtle, basilar membrane, 485-486, 501
 labyrinth, 501
- Two-point stimulation of skin, 615-616
- Two-point threshold for skin, 566
- Tympanic membrane (*see* Eardrum)
- Tympanic muscles (*see* Middle-ear muscles)
- Tympanic scala, 11
- Uncertainty of measurements, 672
- Undertones, 114, 197, 476
- Utricle, 452, 678
- Van Eyck, M., 695
- Velocity, perception by ear, 305-312
 of wave motion in medium, 495-496
 of waves in cochlea, 456-457
- Vestibular organs, 485
 microphonics in, 695
 tonal stimulation, 424, 678
 (*See also* Saccule; Utricle)
- Vestibular scala, 11
- Vibrating electrode, 636, 672-673, 697, 702-703
- Vibrating fluid column, 695-696
- Vibration, mechanical, phase of, 51-53
 from vocal cords, 186

- Vibration microphone, 151-155, 164-177
 Vibrational echoes on skin, 632-633
 Vibrator, 49-51
 for bone conduction, 133-134, 150-151, 158-159
 Vibratory frequencies, interactions, 606-607
 Vibratory phenomena, beats, 574-575, 578-590
 Vibratory "pitch," basis, 590-598
 Vibratory sensitivity of skin, 545-634
 effect on, of anesthesia, 600
 of bodily location, 607-609
 of duration, 559, 598
 of wave form, 585-586
 fusion frequency, 599-601
 location, 560-562, 597
 magnitude, 615-626
 onset time for, 536
 spread, 571-572
 temporal course, 598, 620
 (See also Skin sensitivity)
 Vierordt, K., 169, 371, 726
 Viscosity, 544
 of perilymph, 434
 Visibility of cochlear structures, 38, 426, 441, 459, 475
 Vision, directionality in, 573-574
 Visual analogy of excitation, 229
 Visual space system, 286
 Vital staining, 35, 488-489
 Vocal apparatus as sound source, 306
 Vocal cords, vibrations from, 186
 Vocal sounds, loudness for groups of persons, 380
 Vocalization, of animals, 181
 hearing by bone conduction, 181-191
 isolation of ear in, 201
 skull vibrations in, 187-190
 sound pressure, 183
 Voice regulation, 379
 Voigt, W., 726
 Volleys, neural, 590-603
 Voltage attenuation, in cochlea, 661, 664-666
 in homogeneous fluid, 661-664
 Voltage pattern in cochlea, 653-672, 685-686
 Volume displacement of cochlear structures, 436
 Volume elasticity of round-window membrane, 435-438
 Vrijdaghs, J. J. H., 337, 727
 Waar, A. G. H., 727
 Waetzmann, E., 60, 74, 108, 134, 138, 148, 258, 267, 321, 332, 348, 360, 369, 383, 403, 433, 723, 727
 Wagner, K. W., 60, 727
 Warble tone, 383-384
 (See also Modulation)
 Warming of skin, effect on sensitivity, 626-627
 Water bath for cochlear dissection, 28
 Watson, N. A., 148, 164, 178, 179, 727
 Wave motion, direction of travel, 510-525
 effects of absorbent surfaces on, 392-399, 525
 energy flow in, 510-524, 530-532
 equations for, 495
 forms, 495
 phase relations in, 494
 Wave patterns as sum of two tones, 579-582
 Waveform, perception on skin, 585-586
 Weber's test, 135
 Weber-Fechner law (see Fechner's laws)
 Wegel, R. L., 139, 265, 332, 414-415, 417, 727
 Wenthe, E. C., 369, 387, 727
 Werner, C. F., 727
 Wertheimer, M., 253, 254, 301, 317, 720
 West, W., 267, 727
 Wever, E. G., 512, 526, 533, 575, 577, 641, 684, 685, 727, 728
 Wever-Bray effect, 501
 Wheatstone bridge, 71-72
 White, S. D., 69, 725
 Wiechert, E., 655, 728
 Wien, M., 564
 Wiener, F. M., 728
 Wiener, O., 525, 728
 Wilkinson, G., 406, 728
 Wilska, A., 728
 Windows, observational, 32
 Wisner, A., 577, 722
 Wittmaack, K., 409, 728
 Wollaston wire used in thermophone, 66
 Wrightson, T., 114, 728
 Yantis, P. A., 722
 "Z" character, 345, 351
 Zeluff, V., 667, 723
 Zimmermann, K. W., 487, 728
 Zinc oxyphosphate cement, 21
 Zoller, K., 169, 728
 Zurmühl, G., 337, 463, 728
 Zwislocki, J., 512, 533, 728
 Zygomatic process, 430



